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LINKING FISH TRAITS AND DISTRIBUTION WITHIN HETEROGENEOUS STREAM LANDSCAPES: INTRA-SPECIFIC VARIATION AND HABITAT SELECTIVITY

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LIER LES TRAITS DES POISSONS ET LEURS DISTRIBUTIONS À L'INTÉRIEUR DE PAYSAGES HÉTÉROGÈNES DE COURS D'EAU: VARIATION INTRASPÉCIFIQUE ET SÉLECTIVITÉ DE L'HABITAT

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" Nature is a language and every new fact one learns is a new word; but it is not a language taken to pieces and dead in the dictionary, but the language put together into a most significant and universal sense. I wish to learn this language- not that I may know a new grammar, but that I may read the great book which is written in that tongue."

- Ralph Waldo Emerson

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RESUMÉ

Depuis longtemps, les écologistes s'intéressent aux patrons de distributions des espèces et des individus dans les paysages hétérogènes et tentent d'en comprendre les processus sous-jacents. Alors que les études passées s'appuyaient principalement sur l'identité des espèces, les approches actuelles se basent sur un intérêt renouvelé envers les traits des espèces. Les approches basées sur les traits permettent une compréhension fonctionnelle de la structure des communautés et des populations et de leurs liens avec l'environnement ainsi qu'une généralisation plus aisée des résultats. Un des facteurs dont le rôle est peu considéré, mais ayant le potentiel d'influencer la distribution des individus et la structure des communautés de façon importante, est la variation intraspécifique. En effet, même si la variation entre individus est reconnue comme étant potentiellement adaptative étant donné que les filtres biotiques et abiotiques agissent au niveau de l'individu, la plupart des études centrent leurs explorations sur la moyenne des traits par espèce et les différences interspécifiques. À cet effet, l'objectif de cette thèse était d'explorer la fonctionnalité potentielle de la variation intraspécifique et d'examiner à quel point le phénotype des individus influence leurs distributions dans diverses conditions environnementales. Les cours d'eau et les poissons y résidant sont d'excellents sujets pour ce type d'analyses. En effet, les cours d'eau sont des habitats hautement variables tant spatialement que temporellement contenant des sections présentant des pressions sélectives différentes restreignant potentiellement les phénotypes pouvant s'y trouver. Cette thèse comprend quatre chapitres, trois expérimentaux et un théorique. Le chapitre I explore l'interaction entre la distribution spatiale des ressources et la densité de la population sur la génération de variation de croissance à l'intérieur d'une espèce. Le chapitre II se penche sur la façon dont les individus avec différents phénotypes diffèrent dans leurs décisions non aléatoires de se déplacer et dans leurs sélections d'habitats en fonction de la densité de la population. Le chapitre III explore le potentiel pour une telle sélection d'habitats en fonction du phénotype de s'opérer au niveau de la communauté, et ce, en observant l'assemblage des communautés de différentes sections d'habitats d'un tronçon d'un cours d'eau en fonction du temps. Finalement, le chapitre IV considère les mouvements à une échelle plus large que le cours d'eau et explore la dispersion dans les métacommunautés. Ce chapitre met en perspective les difficultés auxquelles font face les chercheurs dans la quantification de la dispersion et dans la distinction de ce processus des autres facteurs pouvant générer des signaux spatiaux. Les résultats de ces chapitres montrent que les variations de croissance à l'intérieur d'une espèce peuvent découler de l'interaction entre la distribution des ressources et la densité. De plus, la morphologie des individus influence leur capacité compétitive et ceux-ci ont l'habilité de sélectionner leurs habitats en fonction de leur capacité de nage et de la densité. En ce qui a trait aux communautés, l'assemblage des phénotypes suit une trajectoire déterministe par rapport à la nature des habitats. Ainsi, cette thèse démontre que la variation

intraspécifique joue un rôle fonctionnel dans la façon dont les individus se distribuent dans les paysages hétérogènes et qu'autant les facteurs biotiques qu'abiotiques peuvent influencer cette distribution.

Mots clés : Dispersion, métacommunautés, sélection d'habitats dépendante du phénotype, densité de population, distribution spatiale des ressources, assemblage des communautés basée sur les traits

SUMMARY

Ecologists have long been interested in investigating the patterns in, and understanding the processes underlying, the distribution of species and individuals across heterogeneous landscapes. While past studies were largely based on species identities, currently there has been a renewed interest in the use of trait-based approaches. Such a trait-based ecology allows for both a functional understanding of community or population structure and its link with the environment as well as results that are more easily generalized. One important factor influencing distribution and structure which remains underappreciated is the role of intra-specific variation; species trait means and inter-specific differences still largely the focus despite individual variation being recognized as potentially adaptive and the individual-level that at which both biotic and abiotic filtering actually occurs. To this end, the goal of this thesis was to further explore the potential functionality of intra-specific variation and investigate the degree to which an individuals phenotype influences its distribution within and across different environmental conditions. An excellent system is provided by the use of streams and stream-fish, streams highly spatially and temporally heterogeneous with habitat sections that place very different selective pressures on the phenotypes able to be present within. This thesis is comprised of four chapters, 3 experimental and one perspective. Chapter I investigated the interaction between the spatial distribution of resource patches within a section and population density for generating intra-specific growth variation; Chapter II then explored how individuals with differing phenotypes may use non-random movement and phenotype-dependent habitat selection for sorting across habitat sections as a function of density, with chapter III exploring the potential for such phenotype sorting to occur at the community level, across habitat sections within a stream reach and as a function of time through community assembly. Lastly, chapter IV shifts from considerations of movement within streams to larger scale dispersal within metacommunities, discussing the potential difficulty facing researchers in quantifying dispersal and disentangling it from other factors which produce spatial signatures. Results from these chapters show that intra-specific growth variation can be produced by the interaction between resource distribution and density where competitive ability is based on morphology, and that individuals have the ability to use phenotype-dependent habitat selection as a function of density and swimming capacity; at the community level phenotypes sorting across habitats and following a deterministic assembly trajectory. Thus this thesis shows that intra-specific variation plays a functional role in determining individual distribution across heterogeneous landscapes and that both biotic and abiotic factors act to structure distribution.

Keywords: Metacommunity dispersal, phenotype-dependent habitat selection, population density, spatial resource distribution, trait-based community assembly

INTRODUCTION

0.1 Trait-based ecology and landscape distribution

Ecologists, population and community alike, have long been interested in investigating the patterns in, and understanding the processes underlying, the distribution of species and individuals across heterogeneous landscapes. In the past, studies to this end largely focused on, and reported, species identities while describing the presence/absence of species and differing abundances of individuals across different environmental conditions. Such a use of species names, however, left the results found and conclusions drawn both highly contingent on the species pool and system investigated, as well as relied heavily on the researchers' (and readers) knowledge of the ecology of the particular species in order to understand its patterns of distribution (McGill *et al.*, 2006; Weiher and Keddy, 1995).

Currently, ecology is seeing a renewed interest in, and a resurgence of the use of, trait-based approaches, proposed as a way to overcome such previous contingencies. Here, rather than species identities, traits and in particular functional traits, defined as any morphological, physiological or behavioural feature which influences organism performance (Frimpong and Angermeier, 2010; McGill *et al.*, 2006; Violle *et al.*, 2007, 2012), are measured and linked to distribution within and across the landscape. As different species within the same environment may share similar traits (e.g., fusiform body morphology of stream-fish within high-flow areas; Gatz, 1979; Leavy and Bonner, 2009), or individuals of the same species across different environments may differ (e.g., resource polymorphisms; Smith and Skúlason, 1996), trait-based studies allow both a functional understanding of community or population structure and its link with environmental characteristics, as well as provide results that are

potentially generalizable beyond the particulars of the species pool and system investigated (McGill *et al.*, 2006; Weiher and Keddy, 1995).

Just how species and individuals, and in association traits, become distributed across heterogeneous landscapes and are ultimately found within observed communities and populations is conceptualized as being based on their ability to pass through a series of hierarchical selective filters. First, at the regional scale, individuals which are part of the regional species pool must be able to arrive at, disperse into, a location (i.e., habitat patch) (Tonn, 1990). Species, then, must first pass through an abiotic (environmental/habitat) filter, which itself may select at multiple spatial and temporal scales, restricting the presence of species and range of traits to only those adapted to the habitat patch conditions (Poff, 1997; Tonn, 1990), before finally passing through a biotic filter (e.g., competition) which acts to limit the similarity of individuals and traits ultimately present within the patch (Cornwell and Ackerly, 2009; Jackson *et al.*, 2001; Poff, 1997; Violle *et al.*, 2012).

While it is the influence of the final biotic filter which has formed the basis of much of ecological theory in the past, competition considered the main structuring mechanism, it is now recognized that the abiotic filter may also play a large role in determining community and population structure (Grossman and Sabo, 2010); studies conducted at larger scales or within more harsh (selective) environments (e.g., increased disturbance, decreased productivity) finding a greater relative role of abiotic versus biotic influences (Fukami and Lee, 2006; Jackson *et al.*, 2001; Peres-Neto, 2004). Indeed investigations of the relative role of different filters now underlie several frameworks, metacommunity theory interested in the relative role of space (used as a proxy for dispersal) and the environment in structuring large scale distribution (Cottenie, 2005; Leibold *et al.*, 2004), community assembly studies in the relative role of habitat filtering and limiting similarity in structuring trait variances

(range and spacing) (Cornwell *et al.*, 2006; Kraft *et al.*, 2008), habitat selection in the role of density for the use of optimal versus suboptimal habitats (Morris, 2003; Rodríguez, 1995).

0.2 Intra-specific variation and the functionality of phenotype

Despite the renewed interest in trait-based ecology, one important factor influencing individual distribution and community structure which remains underappreciated, and is still largely overlooked, is the role and presence of intra-specific variation. Indeed much of ecology describes and compares species based on mean trait values (Albert *et al.*, 2010b; Bolnick *et al.*, 2003; Cornwell and Ackerly, 2009; Messier *et al.*, 2010), where average values are often computed using individuals found throughout the landscape, across the environmental gradient studied (e.g., Cornwell *et al.*, 2006; Siefert, 2012). Such an averaging, however, assumes that all individuals can be considered equivalent and interchangeable and that any variation that exists across this gradient has no ecological consequences (Bennett, 1987; Bolnick *et al.*, 2003, 2011); the use and comparison of species means within community ecology implying that it is at the species level at which abiotic and biotic filtering occurs.

Of course, however, conspecifics cannot be considered equivalent, populations of the same species located at different points along environmental gradients found to have different mean trait values, intra-specific variation responsible for shifting trait values as a function of the environment (Cornwell and Ackerly, 2009; Jung *et al.*, 2010; Siefert, 2012); variation due to underlying genetic diversity and/or phenotypic plasticity (Jung *et al.*, 2010; Siefert, 2012; Violle *et al.*, 2012). In addition, not only do populations vary across the landscape but so do individuals within a population, where this variation is increasingly recognized as potentially adaptive (Halama and

Reznick, 2001). Indeed, overall population niche width is a function of such individual variation, individuals specialized and trading-off for the use of a specific subset of the resources or environments used by the population as a whole (Bolnick *et al.*, 2003; Futuyma and Moreno, 1988; Robinson *et al.*, 1996) where even subtle morphological differences, detectable only with the use of multivariate statistics, have significant consequences for individual fitness and distribution (Halama and Reznick, 2001; Robinson *et al.*, 1996).

It is at this individual-level, then, and not the average species-level, that both interactions within the population or community occur, intra-specific competition stronger than inter-specific, as well as the level at which environmental selection and sorting takes place (Clark, 2010; Jung *et al.*, 2010; Siefert, 2012; Violle *et al.*, 2012). As such, the goal of this thesis was to further explore the potential functionality of intra-specific variation and investigate the degree to which an individuals phenotype influences its distribution within and across different environmental conditions. Here, such phenotype-habitat relationships were explored at three different levels: 1) the distribution of individuals with respect to resource distribution, 2) the habitat selection of individuals among habitat types; and 3) the assembly of communities and re-colonization of individuals as a function of habitat selectivity.

As within this thesis research was conducted using streams and stream-fish as a model system and using geometric morphometrics as the method with which to capture/analyze functional morphology, these topics serve as the basis of the following sections. Here, specifics regarding stream habitat characteristics and the association and sorting of fish functional traits are also discussed. Lastly, the final section of this introduction outlines each of the chapters which comprise this thesis as well as how they connect to each other.

0.3 The use of streams and stream-fish

The use of streams and stream-fish provide the perfect system in which to explore the potential relationships between habitat characteristics and the distribution decisions made by, and functional morphology of, the individuals and species within. Indeed streams are highly spatially heterogeneous, composed of discrete habitat sections which can be easily visually identified based on differences in depth, water flow and substrate composition; riffles shallow areas of high water velocity over often rock-boulder substrate, pools deep areas of slow current composed of sand and runs intermediate between the two (Brown and Brussock, 1991; Lamouroux and Cattanéo, 2006; Rodríguez, 1995). Such sections can be found to regularly repeat, nested within the larger stream reach, and thus provide for natural replicates; note this hierarchical structure extends across multiple scales, microhabitats nested within sections, reaches nested within stream segments, segments within stream systems and so on, and thus there exist multiple abiotic filters (Frissell *et al.*, 1986; Poff, 1997). In addition streams are also temporally heterogeneous, varying most notably in water flow (i.e., drought versus flood), where the impacts of this highly structuring variable (Grossman and Sabo, 2010; Hoeinghaus *et al.*, 2007; Poff and Allan, 1995) are most felt within riffles, pools less disturbed by periods of high flow as well as under less risk of drying during drought (Brown and Brussock, 1991). Here it is worth noting that due to such strong abiotic pressures it has been questioned within such systems whether biotic factors in fact play a role in structuring distribution (Jackson *et al.*, 2001; Peres-Neto, 2004).

Very different selective pressures are thereby placed upon the individuals and species found within the different habitat sections, strong species and phenotype-habitat associations found despite such fluctuations (Belica and Rahel, 2008; Lamouroux and Cattanéo, 2006; Poff and Allan, 1995; Pyron and Lauer, 2004). Indeed due to

increased water flow and in association energetic demands, riffle sections are perhaps more selective than pools, requiring individuals within to have a greater swimming capacity and/or the ability to hold station (Lonzarich *et al.*, 1998; Rodríguez, 1995). Such swimming requirements are found to be reflected in the morphology of individuals found within such areas, mid-water column riffle species having streamlined fusiform body shapes and larger forked caudal fins reflecting their increased swimming capacity (Gatz, 1979; Leavy and Bonner, 2009), benthic species often having wider pectoral fins adapted for the use of braking upon the substrate (Facey and Grossman, 1992; Gatz, 1979). Pool species, on the other hand, instead often have laterally-compressed deeper bodies allowing for their increased maneuvering and turning stability (Gatz, 1979; Leavy and Bonner, 2009; Webb 1984). While fish move through the system, populations known to be composed of a fraction that is mobile and another stationary (Belica and Rahel, 2008; Petty and Grossman, 2004; Rodríguez, 2002; Skalski and Gilliam, 2000), such movements may then be constrained more-so for some species than others, riffle species potentially able to move through and sample all habitats, pool species, instead found to be impeeded by the demands of riffles (Lonzarich *et al.*, 2000; Schaefer, 2001); the ability of fish to be marked and re-captured allowing for the tracking of such movement patterns and distribution decisions.

0.4 The use of geometric morphometrics

While traditionally morphological measurements in ecology have been based on various linear calculations of the length between morphological features (Douglas and Matthews, 1992; Gatz, 1979; Winemiller, 1991) this technique has several drawbacks where measurements (traits) are necessarily univariate, often highly correlated with each other (see Gatz, 1979), and to a large degree capture size rather than shape (Zelditch *et al.*, 2004), although this effect can be removed through

statistical techniques (Adams *et al.*, 2004; Douglas and Matthews, 1992; Peres-Neto and Magnan, 2004). In addition such measurements are time consuming and thus have been proposed to be best made on preserved individuals (Maderbacher *et al.*, 2008), precluding the ability for the study of morphological change, or the release and subsequent tracking of the individual back in the system. In contrast the use of geometric morphometrics allows the capture of morphological shape information from photographs which can be taken of anesthetized individuals, the variables produced multivariate in nature and devoid of the influence of size and has been found to be able to capture even subtle variation in shape (Kassam *et al.*, 2003).

Indeed geometric morphometrics uses the position within a Cartesian system of two-dimensional landmarks placed on photographs of individuals in order to garner shape information. Firstly landmarks are selected based on several criteria, that they are homologous, repeatable, have the same relative position among individuals, allow for consideration of all possible shape differences and fall within the same plane (Zelditch *et al.*, 2004). Next the landmarks are superimposed, in order to factor out size, using one of several available methods, the most widely used, generalized orthogonal least squares Procrustes superimposition (GLS) (used within this thesis) scales, rotates and translates the landmarks in order to obtain the minimum sum of squared differences between the landmarks for individuals within the analysis (Adams *et al.*, 2004; Rholf and Slice, 1990; Zelditch *et al.*, 2004). Lastly, a principal component analysis of the rotated configurations is conducted producing partial warps, orthogonal axes which can be used as morphological variables directly within any statistical analysis where the use of deformation grids allows for the visualization of relative morphological differences (Adams *et al.*, 2004; Senay, 2009; Zelditch *et al.*, 2004).

0.5 Thesis outline

To re-iterate, the goal of this thesis was to explore the potential functionality of intra-specific variation and determine the degree to which this influences the distribution of individuals within and across different environmental conditions. To this end this thesis is comprised of four chapters, three experimental and one perspective:

Chapter I: The interaction between the spatial distribution of resource patches and population density: consequences for intra-specific growth and morphology

Chapter II: Population density and non-random phenotype-dependent habitat sorting: the case of stream-fishes

Chapter III: The temporal trajectory of community trait re-assembly: morphological trends as a function of habitat

Chapter IV: Quantifying and disentangling dispersal in metacommunities: how close have we come? How far is there to go?

Within chapter I the potential for the generation of variation as a function of habitat conditions was first explored. To this end, this chapter investigated the potential of the interaction between population density and the spatial distribution of resource patches within the landscape, a currently overlooked structuring factor, to influence the level and degree of intra-population growth (i.e., fitness) variance. Here the degree to which competitive ability was a function of morphology related to swimming ability, rather than fish size as proposed, was also explored. To do so feeding and density experiments were conducted within artificial stream channels where the degree of individual growth within a trial was linked to pre- and post-trial morphology.

Chapter II then explored how individuals with differing phenotypes may sort themselves across habitat conditions. Here the potential for non-random movement and phenotype-dependent habitat selection to account for the phenotype-habitat correlations that are found within temporally varying streams was investigated, as well as the degree to which this mechanism may influence distribution as a function of population density (i.e., intra-specific competition). To this end density manipulations were conducted within an artificial stream comprised of multiple habitat types using stream-fish collected from a single original section. This chapter also explored the degree to which distribution may be influenced by both habitat conditions, manipulations performed within the artificial stream, as well as factors such as growth rate and sampling capacity, a frequency-dependent game model developed.

Chapter III further explored the potential for phenotype sorting, here investigating not only the distribution of phenotypes across habitats but also through time as a function of community assembly. Here the goal of this chapter was to bridge the gap between current groups of assembly studies, those which take a snap-shot trait-based approach and those that look at temporal trajectories however with respect to only composition. To do so a defaunation experiment was performed within a stream reach comprised of multiple habitat types and natural fish re-colonization of habitat sites was followed. Here trait analyses looking at overall morphological trends and within community patterns were conducted at both the level of the entire stream community as well as using, separately, the two most abundant species.

Chapter IV, lastly, is a perspective paper which discusses, at larger metacommunity scales, the potential difficulty facing researchers in quantifying and measuring dispersal and disentangling it from other factors which also produce spatial signatures. Here the direct and indirect methods currently available to capture

dispersal within metapopulations and metacommunities and the type of information they allow are presented along with the current challenges still faced and concluding with a wishlist for future technical advancements.

To summarize, these chapters are organized by and can be viewed as increasing in the scale of consideration, ranging from population level studies of distribution between resource patches within a habitat section in chapter I, movement and sorting across habitat sections in chapter II to community level re-assembly (re-colonization) across a stream reach in chapter III with chapter IV shifting from considerations of movement within streams to larger scale dispersal at the metacommunity level (e.g., between stream systems or lakes). The experimental chapters are additionally linked by the consideration of traits and the potential for both biotic and abiotic factors to structure distribution.

CHAPTER I

THE INTERACTION BETWEEN THE SPATIAL DISTRIBUTION OF RESOURCE PATCHES AND POPULATION DENSITY: CONSEQUENCES FOR INTRA-SPECIFIC GROWTH AND MORPHOLOGY

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1.1 Summary

How individuals within a population distribute themselves across resource patches of varying quality has served as the basis of many theories; the Ideal Free Distribution proposing equal fitness among individuals in a 1:1 ratio with resources, resource defence theory predicting different degrees of monopolization (fitness variance) as a function of temporal and spatial resource clumping and population density. One overlooked landscape characteristic which undoubtedly influences within-population growth variance is its spatial structure, patch distribution changing resource accessibility and thereby the effective number of competitors. Within streams, an individuals ability to monopolize resources (grow) is often linked to fish size, when invariant, however, little is known regarding the morphological characteristics dictating competitive ability for a single resource type. Here we tested whether and how the spatial distribution of resource patches and population density interact to influence the level and variance of individual growth, and if functional morphology (e.g., swimming capacity) relates to competitive ability. Feeding trials were conducted within stream channels using young-of-the-year rainbow trout under three spatial distributions of 9 resource patches (distributed, semi and clumped) at two density levels (9 and 27 individuals). Contrary to expectation, within-trial growth

variance showed opposite patterns across resource distributions, variance decreasing at low but increasing at high population density as patches became clumped; overall growth greater in high density treatments. Such findings were the result of different levels of aggressive or scramble competition. As predicted, both pre- and post-trial morphology were related to within-trial growth, competitive individuals those with larger heads/bodies/caudal fins and less angled pectoral fins, associated with swimming capacity and efficiency. The different degrees of within-population growth variance at the same density level found here, as a function of spatial resource distribution, provides an explanation as to the inconsistencies in within-site growth variance and subsequent population regulation often noted with regards to density-dependence in natural landscapes.

1.2 Introduction

The question of how individuals within a population distribute themselves across resource patches of varying quality (typically type and/or amount of food) has served as the basis of countless studies and many theories across several fields of ecology. Within population ecology, the Ideal Free Distribution (IFD) offers a base-line proposal of this relationship (i.e., distribution across patches) where at equilibrium, competitively equivalent individuals which have perfect knowledge of and the cost-free ability to move throughout the landscape distribute themselves in a 1:1 ratio with resources such that fitness across individuals is equal (Fretwell and Lucas, 1970; Kennedy and Gray, 1993; Lomnicki, 1988). Tests of the IFD, however, have often found good quality patches to be systematically under-used and poor quality patches over-used, leading to unequal fitness amongst individuals (Abrahams, 1986; Kennedy and Gray, 1993). While it is commonly the violation of the IFDs assumption of equal competitive abilities which is suggested to produce this deviation (see Kennedy and Gray, 1993 for alternative assumptions; Lessels, 1995 and Tregenza, 1995 for

examples of alternative IFD models), good competitors occupying under-used good quality patches (Ideal Despotic Distribution; Lomnicki, 1988; Tregenza, 1995), the presence of unequal competitors within a landscape does not necessarily result in variation in resource gain (Grand and Grant, 1994).

Tregenza *et al.* (1996), for example, found that within their experimental 2-patch system a good competitor only had greater fitness than others when densities were low, at high densities fitness differences between individuals decreased due to a switch from contest to scramble competition. Such an influence of the environmental properties (*sensu* Grant, 1993) of a landscape over the ability for an individual to monopolize resources has been investigated to a great extent within the realm of behavioural ecology. Here, at the scale of an individual resource patch, resource defence theory predicts a dome-shaped relationship (though see Grant, 1993 for the potential presence of upper or lower thresholds) between the economic defendability of a resource patch (i.e., monopolization) and the number of potential competitors for it, as well as the degree of resource temporal and spatial clumping (manipulated via patch size) (Grant, 1993; Grant *et al.*, 2000; Robb and Grant, 1997; Ward *et al.*, 2006). While the amount of aggression (i.e., interference/contest competition) and thus the degree of fitness variation within the system is a function of such monopolization (Grant and Guha, 1993; Noël *et al.*, 2005; Weir and Grant, 2004) within-population variation will also depend on resource accessibility (Boujard *et al.*, 2002).

The spatial structure of a landscape, the distribution of resource patches within the system irrespective of quality, is an overlooked characteristic of the landscape (but see Silver *et al.*, 2000) that has the undoubted potential to influence the relative fitness amongst individuals, altering the equitability of resource accessibility. Indeed when patches are spread across the landscape, individuals may be able to settle into

patches with few interactions between competitors, thus leading to more even resource partitioning (access) and fitness (Noël *et al.*, 2005). As patches become clumped in space, however, and the area within which foraging occurs decreases, the effective number of competitors within the population will increase (Fausch, 1984; Noël *et al.*, 2005 through patch number), decreasing the equality of resource accessibility and increasing fitness variation. Within streams, where much of the work regarding density-dependent growth and regulation (i.e., mortality, emigration) has been conducted, within-site growth variance is currently attributed to variation in foraging site quality (Site Quality Hypothesis (SQH); Lobón-Cerviá, 2010; Newman, 1993; Ward *et al.*, 2007); variance in patch quality due to canopy shading influencing invertebrate abundance, water velocity delivering drift and/or aquatic insect emergence and behaviour (Gotceitas and Godin, 1992; Lancaster *et al.*, 2003; Ward *et al.*, 2007; Ward *et al.*, 2009). Thus while variation in patch quality may inherently be linked with variance in the spatial distribution of such patches, patches need not necessarily differ in quality to produce fitness variation. Considerations of the potential influence of spatial resource distribution may provide alternative explanations for patterns of individual distribution currently attributed solely to patch quality.

Which individuals in the population are able to monopolize resources and/or hold good quality patches is a function of their relative competitive ability where within stream fish competitive dominance (i.e., ability to monopolize) is often linked to length/size, larger individuals able to gain access to the best foraging patches (Fausch, 1984; Ward *et al.*, 2006), older individuals outcompeting younger (Kaspersson *et al.*, 2010; Post *et al.*, 1999). Whether the causal order of this relationship is true, however, has recently been questioned by Ward *et al.* (2006) who asked whether such size was in fact the cause or the effect of competitive ability. This is a particularly relevant question within a single young age-class where size may

initially be somewhat invariant but when growth has large impacts for subsequent survival (e.g., overwintering, within-season mortality; Lobón-Cerviá, 2010; Ward *et al.*, 2009). While much research, across many species, has been conducted regarding the influence of morphology on competitive ability for different resources (i.e., resource polymorphism; Araújo *et al.*, 2008; Bolnick, 2004; Edelaar *et al.*, 2008; Smith and Skúlason, 1996), less remains known with respect to the characteristics dictating relative competitive ability for a single resource type when size variation is inconsequential. In such cases, competitive ability may be conferred based on an individuals ability to use its environment more efficiently. Within riffles, where greater water velocity is related to increased resource delivery (Gotceitas and Godin, 1992), an individuals ability to gain resources may thereby be linked to its swimming capacity and ability to hold station against the current (Leavy and Bonner, 2009; Ward *et al.*, 2006).

In this study, we set out to test whether and how the spatial distribution of resource patches and population density interact to influence the level and variance of growth within landscapes and if an individual's morphology relates to their ability to obtain resources (i.e., compete). To do so we conducted feeding trials within flow-through stream channels using young-of-the-year rainbow trout, *Oncorhynchus mykiss*, under three different spatial distributions of 9 resource patches ranging from evenly distributed across the system to clumped within a single location (Figure 1.1). Such trials were conducted at two density levels, low at the level of one individual per patch versus high, 3 individuals per patch. We expected mean growth to be greater within high-density trials due to a decrease in energy expenditure on aggression, as per resource defence theory (Kim and Grant, 2007). Within low-density distributed trials (1:1 competitor to resource patch ratio), we expected distribution to follow an IFD and individual's growth to be most similar (Noël *et al.*, 2005), with within trial variance increasing with the spatial clumping of resource patches due to changes in

effective competitor number (Fausch, 1984; Noël *et al.*, 2005). Lastly, we expected competitive ability, irrespective of density and resource distribution, to be conferred based on swimming ability (Ward *et al.*, 2006) reflected in functional morphology. The potential patterns in growth variances found, both within and across the density levels tested, may provide an explanation as to the inconsistencies in within-site variance (Imre *et al.*, 2010) and subsequent degrees of population regulation (i.e., emigration, mortality) that are often noted with regards to density-dependence in natural landscapes.

1.3 Materials and methods

1.3.1 Species and experimental set-up

We acquired 500 young-of-the-year rainbow trout (*Oncorhynchus mykiss*) (Figure 1.1A) of 5cm in length from Pisciculture des Arpents Verts, Québec, Canada for use in our experiments. When not in use fish were housed within two circular 133L constant-flow tanks (flow at 50% depth=0.25m/s; water temperature=18-19.5°C) on a 12h light: 12h dark cycle (Brown and Brown, 1993) (lights on at 7am) and fed a maintenance ration of dry food pellets (Skretting extruded salmonid feed). Housing conditions were monitored and daily feedings provided by animal care staff at Concordia University, Québec, Canada.

Experimental trials were conducted within four flow-through experimental stream channels (Figure 1.1B) under the same light regime. Each channel was lined to a depth of approx. 2.5cm with small natural-coloured aquarium gravel wherein nine terracotta "saucers" were embedded, flush with the bed of gravel, to act as resource patches. Flow in each channel was held constant across all trials (average flow at 50%

depth=0.15-0.18m/s across channels). Water temperature within the system (approx. 18°C; Li and Brocksen, 1977) was controlled by the amount of de-chlorinated city water entering each channel and was continuously recorded every 15mins by a HOBO temperature/light data logger (Onset Computer Corporation) placed in each channel. Loggers were checked in the morning before feeding and again at the end of the light cycle (average across channels ± SD: week 1 19.1± 0.6°C; week 2 18.7 ± 0.2°C; week 3 17.7 ± 0.8°C; week 4 18.2 ± 0.2°C; and week 5 17.7 ± 0.5°C); temperatures remained within the preferred range for rainbow trout (Wood *et al.*, 2012). To record feeding dynamics throughout the light cycle, digital colour CCD bullet cameras were connected to a surveillance system (GeoVision, Inc.) and mounted directly above each channel; with the exception of recording periods, channels were covered with large-weave netting to prevent fish from jumping out of the channels.

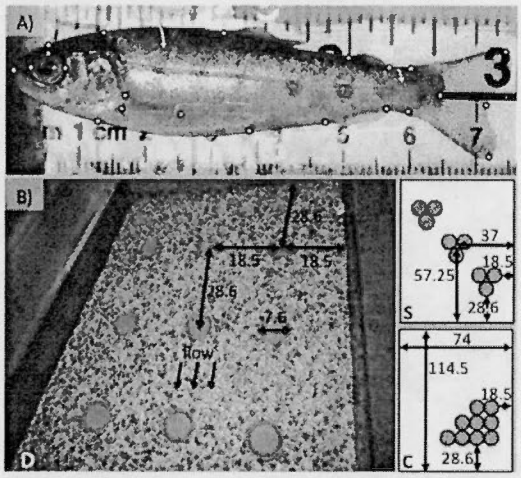

Figure 1.1. Species and spatial resource distributions. A) Young-of-the-year rainbow trout with 22 landmarks used within morphological analyses, curved arrows denote locations of body and caudal width caliper measurements. B) Photo and schematics of spatial resource distributions tested; D is distributed, S semi-clumped and C clumped. Flow denotes the direction of water movement through channels, water depth was approx 18cm, resource patch depth 1.1cm. All measurements within figure are in cm.

1.3.2 Experimental procedure

In order to determine the influence of resource spatial distribution and competitor density on growth, feeding trials were conducted under a 3x2 factorial design testing three different resource distributions (distributed, semi-clumped and clumped, Figure 1.1B) at each of two densities (low n=9 and high n=27) with 3 replicates per treatment. Trials were conducted four at a time from October 14 to November 22 2011, where each week the individuals and treatments tested were both randomly selected and assigned to each stream channel; although individuals were to a small degree length-matched.

Each trial lasted a total of 8 days. On day 1, individuals were selected from housing tanks, anesthetized using a 1 clove oil:10 ethanol mixture (active agent eugenol) (Anderson *et al.*, 1997; Keene *et al.*, 1998) and each given a unique identifier by way of 2 subcutaneous VIE tags (visible implant elastomer; Northwest Marine Technologies) in one or two of 4 fluorescent colours in one or two of several body locations. Individuals were then photographed on one lateral side for pre-trial morphology, weighed for initial mass and measured for initial body and caudal widths (Figure 1.1A). After recovering from anesthesia, individuals were introduced into a stream channel and starved for the day (Olsson *et al.*, 2007). On days 2-7 resources were added once daily to stream channels, evenly divided across the 9 patches, given at a level of 10% (Brown and Brown, 1993) of the total initial mass of individuals within the trial per day in order to encourage growth. Feeding was recorded on day 2 and 7, initial and final feeding, from the time food entered the system until the end of the light cycle. Note that while no mortality occurred as the result of handling or experimental treatment, there were some incidences of individuals jumping out of the channels during recording and thus final densities did not always match initially set levels (low density n=6-10, high density n=21-27; see

also outliers below). When this occurred during day 1 or 2, individuals were identified and the food level for the trial adjusted accordingly. Lastly, on day 8 individuals were starved (Noël *et al.*, 2005) to ensure the same level of gastric evacuation (Currens *et al.*, 1989; Fausch, 1984) and near the end of the light cycle were anaesthetized, identified, weighed for final mass and photographed on the same lateral side for post-trial morphology. Individuals were afterwards returned to a separate holding tank to ensure that no individual was used more than once.

1.3.3 Data analyses

Three growth metrics were calculated for each individual and used as dependent variables within analyses: 1) Individual growth, G_{ind}, calculated as the difference between $\log_{10}$ transformed final and initial mass; 2) Growth variance, G_{var}, calculated as the absolute value of the difference between G_{ind} and the average G_{ind} of the trial in which the individual participated; and lastly 3) Relative growth, G_{rel}, calculated removing the absolute value from G_{var}, classified individuals as having either less or greater growth (negative or positive values respectively) relative to their trial average.

In order to determine the influence of treatment type on overall trial growth and the degree of intra-trial variance, G_{ind} and G_{var} were used within mixed-model analysis of variances (ANOVAs) with density, spatial resource distribution and the density x spatial distribution interaction entered as fixed effects and the week in which the trial was conducted as well as the channel itself entered as random effects. Such random effects were used in order to control for some degree of contingency that may have occurred as a function of random sampling for trial participation and the fact that individuals participating in later weeks had larger initial masses due to growth in housing. In order to ensure that any significant differences between treatment types

with respect to average growth (G_{ind}) or variance (G_{var}) were not an artifact of non-random sampling of individuals, mixed-model ANOVAs were again run using initial mass ($Mass_i$) and initial mass variance ($Mass_{ivar}$) (calculated as per G_{var}) as response variables.

In order to determine if there was an influence of an individual's morphology on their ability to capture or potentially defend resources (i.e., grow) within trials, geometric morphometrics were used to transform photographs into morphological information. To do so 22 landmarks were placed on both pre- and post-trial photographs (Figure 1.1A) using the program tpsDIG2 (Rohlf, 2005a) and converted, separately, into partial warps using the programs Coordgen6 and PCAgen6 (Sheets, 2004a, 2004b). Pre-and post-trial warps were then entered as separate fixed effects within a mixed-model ANOVA using G_{rel} as the dependent variable. Note that 3 individuals, randomly distributed across treatments, were identified as outliers with respect to post-trial morphology and were removed from all analyses. To visualize any morphological differences between G_{rel} classifications (i.e., less or greater growth than their trial average), deformation grids were produced for pre- and post-trial morphologies using the program tpsRegr (Rohlf, 2005b). As competitive ability within fish is often proposed to be a function of length/size (Ward *et al.*, 2006) and the effect of size is removed through standardization with the use of geometric morphometrics (Zelditch *et al.*, 2004), a series of regressions were performed for each treatment type testing the relationship between G_{ind} and each of $\log_{10}$ transformed initial mass ($Mass_i$), initial standard length ($Length_i$), initial body width ($BodyW_i$) and initial caudal width ($CaudalW_i$). Correlation significances were determined with the use of mixed-model ANOVAs using G_{ind} as the dependent and each variable, separately per treatment, as the fixed effect, the inclusion of random factors (as above) allowing for the consideration that replicates differed in variances; values were zscore transformed prior to use within regressions and mixed-model ANOVAs

(Schielzeth, 2010). All Mixed-model ANOVAs were run using the nlme package (Pinheiro *et al.*, 2012) in R version 2.13.0 (R Development Core Team, 2011) and regressions were performed using Statistica 6.0 (StatSoft).

The spatial dynamics of resource patch use and types of competitive interactions used by individuals during feeding were observed from recordings of the final feeding (day 7) only, as it was assumed that recorded behaviour had at this point become established (Noël *et al.*, 2005). The first hour of all of such videos were observed and showed similar interactions and spatial dynamics; only the final replicate of each treatment type is reported. Spatial feeding dynamics were recorded as the number of seconds within a minute that at least one individual was at least ½ body length within each patch, recorded every 5 minutes for the first 15 minutes of feeding during which time feeding activity was at its highest. Information garnered is presented in Figure 1.3. Due to issues of low video quality and the tightly packed quick movements during feeding at high densities, only qualitative differences in interaction types (agonistic versus scramble) and frequencies across treatments were recorded. Interactions were considered aggressive if chasing occurred (defined as per Kim and Grant, 2007; Robb and Grant, 1998) or to reflect scramble (exploitative) competition should no direct interaction occur with individuals only indirectly reducing the amount of available resources (Weir and Grant, 2004).

1.4 Results

Mixed-model ANOVAs indicated that the degree of individual growth (G_{ind}) within trials differed as a function of density alone with average growth greater within high versus low-density treatments, irrespective of the type of resource spatial distribution (Table 1.1 and Figure 1.2A). Most interestingly, the degree to which such growth

varied amongst individuals within trials (G_{var}) was significantly dependent upon all factors, spatial treatment, density and their interaction (Table 1.1) and showed opposite trends, variance decreasing at low densities however increasing at high densities as resources became more spatially clumped (Figure 1.2B). Greater within-trial growth variance in high density spatially clumped treatments occurred in part because 14 individuals within these trials lost weight throughout the trial and thus finished with negative growth; only two individuals lost weight in the distributed and one each in the semi-clumped and clumped treatments at low densities. Significant differences in growth mean and variance as a function of treatment type were not the result of non-random individual sampling as average initial mass and initial mass variance did not differ among treatments (Table 1.1).

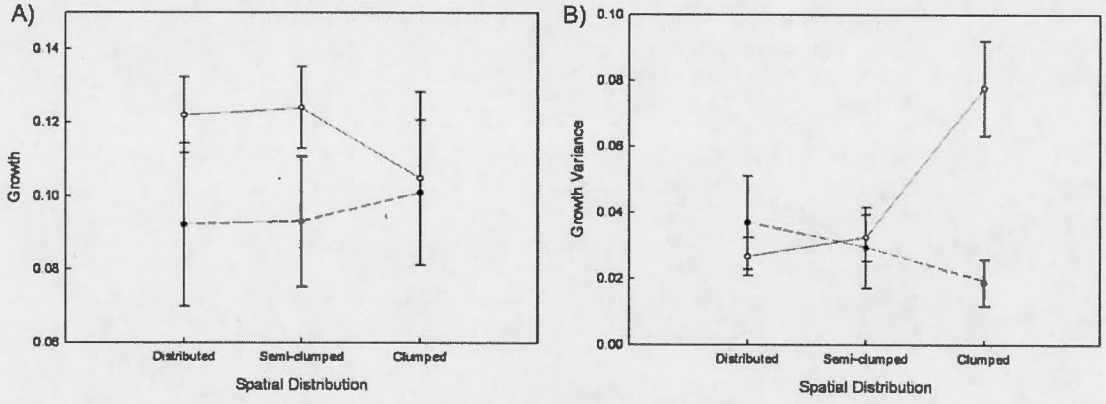

Figure 1.2. Results from mixed-model ANOVAs of growth outcomes of trials. A) Growth (G_{ind}) outcome for trials as a function of spatial and density treatments. B) Variance in growth (G_{var}) outcome for trials as a function of spatial and density treatments. Open circles denote high density, filled low-density trials, error bars are 95% confidence intervals.

Table 1.1. F-values from mixed-model ANOVAs regarding the influence of treatment type and morphology on within-trial growth. Numbers in brackets are degrees of freedom.

	Factor	Dependent			
		G_{ind}	G_{var}	$Mass_i$	$Mass_{ivar}$
Treatment	Space (2)	0.168	8.677*	0.531	0.852
	Density (1)	6.938*	5.904*	0.481	0.005
	SxD (2)	0.779	9.56*	0.017	1.148
		G_{rel}			
Morphology	Pre-trial (40)	1.628*			
	Post-trial (40)	3.230**			

* $p \leq 0.05$
** $p \leq 0.001$

Observation of feeding videos recorded during the final feeding revealed different spatial dynamics (Figure 1.3) and types of individual interactions as a function of density and resource distribution. Overall more agonistic interactions (interference competition) were noted within low-density trials, decreasing as spatial resource clumping increased. Within distributed trials, a single individual tended to chase and exclude others from the entire resource arena, wherein foraging attempts were made mainly at patches where foraging had already occurred (reflected in the location and shading of patch use within Figure 1.3). Conversely, individuals within clumped resource distributions circulated through patches utilizing only scramble/exploitative competition; semi-clumped distributions were intermediate with scramble around and minor chases between patch clumps across which individuals tended to again move and forage together. Opposite interactions were observed from videos of high-density treatments where scramble competition predominated in all resource distribution types, individuals divided relatively evenly amongst and continually circulating over all patches. Despite such prevalence, minor chases were noted within semi-clumped trials when an individual would attempt to monopolize a single clump of patches (upper left-hand grouping Figure 1.3). Several instances of aggression also occurred, at later stages of feeding, both within and outside of the resource arena within

clumped resource trials wherein, throughout, several individuals never appeared to attempt foraging. Across all treatments, when not foraging, individuals remained within the downstream portion of the stream channel.

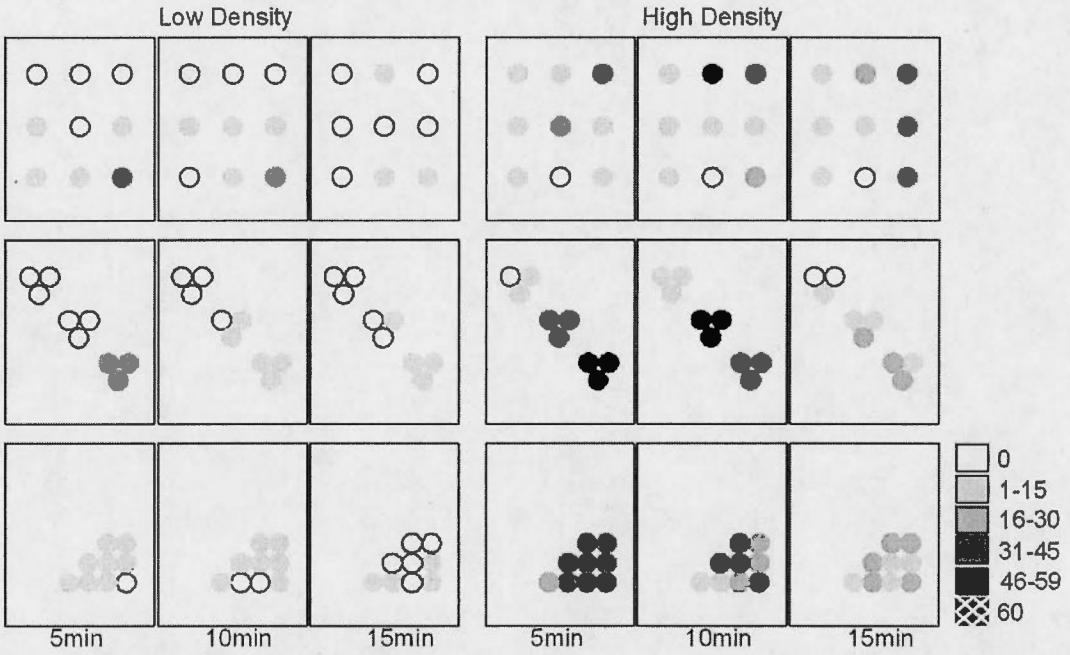

Figure 1.3. Spatial feeding dynamics of individuals throughout the first 15 min of feeding. Shading is based on the number of seconds within 1 min that at least ½ body length of at least one individual was within the resource patch.

The degree to which individuals grew within a trial, irrespective of treatment, was found to be a function of their morphology, as evidenced by outcomes from a mixed-model ANOVA, both pre- and post-trial morphology differentiating between individuals of opposite relative growth (G_{rel}) (Table 1.1). Such effects could also be seen in deformation grids of pre- and post-trial morphology as a function of G_{rel} (Figure 1.4) where the primary differences between groups in pre-trial morphology were differences in pectoral fin angle, head/body and caudal fin size and head shape and body height with regards to post-trial morphology. Growth was, with few

exceptions, unrelated to initial fish length/size, regressions overall largely non-significant (Table 1.2).

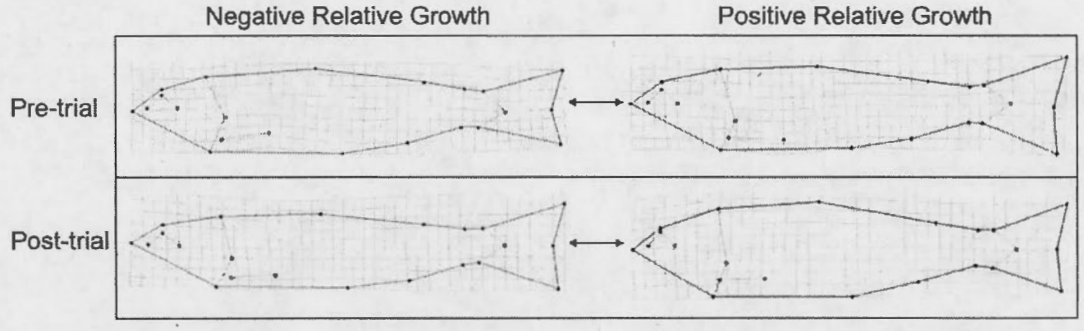

Figure 1.4. Morphological differences between individuals with negative or positive (less or greater) growth relative to their trial average (G_{rel}) as a function of pre- or post-trial morphology. In order to highlight differences variation is depicted at 10x the observed range.

Table 1.2. Correlation coefficients (r) from regressions of the relationship between individual growth (G_{ind}) and initial size variables. D is distributed, S semi-clumped and C clumped spatial resource distributions; numbers in brackets are the combined number of individuals in the replicates of that treatment type.

	Low Density			High Density		
	D (26)	S (24)	C (22)	D (77)	S (73)	C (77)
$Mass_i$	0.368	0.105	0.746*	0.486*	0.299	-0.006*
$Length_i$	0.470*	0.169	0.733	0.565*	0.391**	-0.022*
$BodyW_i$	0.323	0.188	0.688	0.405	0.350*	-0.003
$CaudalW_i$	0.309	0.098	0.659	0.229	0.262	0.072

* $p \leq 0.05$
** $p \leq 0.001$

1.5 Discussion

The main goal of our study was to test whether the spatial distribution of resources and population density interact in determining the growth and growth variance (i.e., fitness) amongst individuals within a landscape. We found that this interaction can generate different levels of fitness variation within a population through differences in the types of competition used, causing individuals with specific morphologies (i.e., phenotype) to be conferred more or less relative fitness dependent on treatment. Such results have important consequences for the demographics of populations and degree of regulation expected in natural systems of varying structure, explaining several inconsistencies found in the literature regarding density-dependent growth patterns (see 1.5.3 Implications for population regulation).

1.5.1 Inter-treatment growth patterns: variance and competition

Results from our study clearly show that the spatial distribution of resource patches themselves, irrespective of quality, can influence the degree and distribution of relative fitness (i.e., growth) amongst individuals within a population through changing the effective number of competitors for patches within the system. Here, contrary to expectation, opposite patterns of intra-population (trial) variances in growth were found across resource distributions between the two densities tested, variance greatest when resources were clumped within high-density trials but when resources were distributed at low densities. Since within low-density spatially distributed trials the number of resource patches was equivalent to the number of individuals, we expected distribution to follow an IFD (as per Noël *et al.*, 2005) and fitness amongst individuals to be most similar. Instead, as evidenced from recordings of feeding, the variance found was a function of both a single individual attempting to defend all patches within the system and others attempting to forage at only those

patches already sampled. This suggests a potential difficulty for less competitive individuals to find resource patches within our system, a phenomenon which may not have occurred in other studies who tend to test patch use at a smaller scale (e.g., Noël *et al.*, 2005; Tregenza *et al.*, 1996). As the spatial distribution of patches became increasingly clumped at low-densities, increasing the effective number of competitors for patches, interactions were observed to switch from agonistic to scramble competition accounting for the decrease in growth variance, defense too costly with increasing competitor pressure (Grant, 1993; Grant and Guha, 1993; Kaspersson *et al.*, 2010; Syarifuddin and Kramer, 1996; Tregenza *et al.*, 1996).

Accordingly, scramble competition was observed to predominate within high population density trials (Brown *et al.*, 1992; Jobling and Baardvik, 1994), individuals cycling in and out of resource patches (Robb and Grant, 1997). As aggression has been found to have important associated fitness costs, increasing energy expenditure, social stress and resource loss while defending (Kaspersson *et al.*, 2010; Kim and Grant, 2007; Li and Brocksen, 1977) this provides an explanation for the greater average growth, irrespective of resource distribution, that was found within high versus low-density trials. That average growth was most similar between densities at clumped resource distributions, within low density trials when scramble competition occurred and growth was greater (most similar), within high density trials when growth was lower due to loss of weight (most variant) and minor aggression, further supports this assertion. Despite the fact that scramble competition is proposed to allow for a more even distribution of resources amongst individuals and to occur when intruder pressure (i.e., density) is high (Boujard *et al.*, 2002; Grant, 1993; Jobling and Baardvik, 1994; Weir and Grant, 2004), here an upper limit to such a relationship was found. Indeed the greatest degree of growth variance was found within high-density clumped resource distribution trials, when the effective competitor number was greatest. The associated decrease in equal resource

accessibility which has been found to occur at high densities (Boujard *et al.*, 2002; Syarifuddin and Kramer, 1996) not surprisingly led to individuals ceasing to feed, generating negative growth (Grant and Kramer, 1990; Li and Brocksen, 1977) where the noted aggression within such trials amongst non-feeding individuals potentially reflected a "last ditch effort" response. Unlike at overall low densities, within distributed trials where resources were the most accessible, scramble competition, rather than aggression, allowed individuals to spread themselves somewhat more evenly among patches, though still not perfectly approximating an IFD.

Such results call attention for the potential need for context dependency with the use of integrated metrics, such as the recently formulated competitor-to-resource-ratio (CRR), proposed as a way to predict the degree of aggression (resource monopolization) through relating the ratio of potential competitors to the amount of resources within the system (Grant *et al.*, 2000). Noël *et al.* (2005) recently manipulated CRR level through altering the number of patches within which a constant amount of food was distributed. Here, if we take the spatial distribution (i.e., clumping) of patches to also change the effective number of patches, as may be reasonable since this changes the effective number of competitors, then this study tested CRR levels of 1, 3 and 9 within low density treatments and 3, 9 and 27 within high density treatments; with very different levels of monopolization/aggression found at overlapping CRR levels. As CRR changes as both a function of the number of competitors at a constant resource level and the amount of resources at a constant density, knowing just the CRR level without context, especially comparing across experimental or natural systems, may not alone be an accurate predictor of the degree of within population growth variance (i.e., degree of monopolization).

1.5.2 The influence and shaping of phenotype

While competitive ability is often suggested to be related to body size, larger individuals more efficient foragers able to outcompete smaller individuals (Kaspersson *et al.*, 2010; Post *et al.*, 1999; Ward *et al.*, 2006), here we found, overall, no significant relationship between an individuals level of growth and their initial mass, length, body or caudal width. Instead, competitive ability was conferred through phenotype where pre-trial morphology, the body shape individuals had initially, dictated which type of individual would be able to gain the most resources within trials. Individuals that experienced greater growth than the average of their trial were those with deeper heads/bodies and larger caudal fins indicating greater swimming ability (Gatz, 1979; Ojanguren and Braña, 2003; Peres-Neto and Magnan, 2004) and turning stability (Webb, 1984), and whose pectoral fins were more flatly angled, potentially indicating both the ability for more efficient maneuvering (Drucker and Lauder, 2003) and to reduce energy expenditure through holding position against current on the substrate (Fausch, 1984). As swimming ability has been proposed to relate to competitive ability in both scramble and contest (aggressive) contexts (Ward *et al.*, 2006) such phenotypic characteristics account for the greater growth these individuals were able to gain relative to others within trials.

Post-trial morphology was also found to be highly correlated with trial growth possibly reflecting both the relative effects of the amount of growth on body shape in and of itself (Borcherding and Magnhagen, 2008; Currens *et al.*, 1989), as well as potential investment in plasticity (i.e., morphological modulation) by individuals who had greater levels of growth (Olsson *et al.*, 2006, 2007), acting to further increase their competitive ability. As equivalent body shape differences may be found with regards to both cases, it is not possible to differentiate such underlying causes of post-trial morphological differences. Indeed, more dorsally placed eyes and greater body

height amongst individuals with greater relative growth reflect benthic habitat use (Gatz, 1979; Mason *et al.*, 2007), where food was located within the system, and increased swimming ability and turning stability (Ojanguren and Braña, 2003; Peres-Neto and Magnan, 2004; Webb, 1984) indicating competitive ability, while a more slender body and longer head amongst those with less relative growth potentially reflects under-nourishment (Borcherding and Magnhagen, 2008; Olsson *et al.*, 2007; see Currens *et al.*, 1989 for full body shape-nourishment considerations).

1.5.3 Implications for population regulation

Within natural landscapes growth is often found to be negatively density-dependent following a negative power curve, sites with higher population densities having lower average (Grant and Imre, 2005; Jenkins *et al.*, 1999) but greater growth variance (Keeley, 2001; Lobón-Cerviá, 2010; Newman, 1993). When density-dependent population regulation (i.e., emigration, mortality) occurs, the resulting patterns in growth are much more variable, studies reporting from negative power curves, negative linear relationships of varying strength to no relationship between average growth and density (Imre *et al.*, 2005; Jenkins *et al.*, 1999; Keeley, 2001; Newman, 1993; Post *et al.*, 1999), with little consistency in the associated variance-density relationship (Imre *et al.*, 2010). As here we found different degrees of within trial variance at the same overall population density as a function of the spatial distribution of resource patches, our results have the potential to shed light on such inconsistencies in natural systems.

Greater degrees of population regulation and consequent redistribution of individuals across the landscape are expected when growth variance within the population is large. Thus, for example, within high population density distributed trials, where

growth was the most similar across individuals, we may expect relatively little pressure for emigration, such sites potentially able to support a greater number, and by extension phenotypic diversity, of individuals. Conversely, within clumped trials, where the number of effective competitors and therefore variance was higher, we may expect instead much greater degrees of mortality and emigration, competitive phenotypes able to remain in the site while non-competitive individuals emigrate to others with less competitive pressure (as here competitive phenotype related to swimming ability this may be akin to adaptive habitat matching; Bolnick *et al.*, 2009; Edelaar *et al.*, 2008) (Jenkins *et al.*, 1999; Keeley, 2001); intra-specific competition often leading to habitat and resource niche expansion (Araújo *et al.*, 2008; Bolnick, 2004; Lobón-Cerviá, 2010; Ward *et al.*, 2006). Thus the relationships between average growth and site density resulting from population regulation of high density sites with different spatial distribution of resources, and thus competitive pressures, may account for the above inconsistencies; a negative power curve remaining in the case of high density distributed structure, a more weakly negative relationship in the case of semi-clumped, to no relationship when sites have clumped resource distributions.

Note that while we found positive instead of negative density-dependent growth such a finding is common within experimental systems where food is given as a percentage of system biomass and therefore proportional to density (Brown *et al.*, 1992). Within natural systems site-resource levels are proposed to be constant across densities (Kaspersson *et al.*, 2010) where low density sites have a greater amount of resource relative to competitor number than high density (Ward *et al.*, 2007). Should we have provided resource levels more in line with natural systems it is conceivable that we would have also found negative density dependence, the potentially lower level of associated variance at low densities still leaving the above implications intact.

Findings of this study show the potential for the spatial structure of resource patches within the system themselves, irrespective of other potentially varying characteristics (i.e., resource quality, patch size), to influence population growth through changing the effective number of competitors within the system and therefore the degree to which competitive ability (phenotype) confers enhanced fitness. Undoubtedly such characteristics of the system interact to influence distribution, where here knowing either the overall population density or the spatial distribution of resources within a trial was not enough to predict growth patterns; although the phenotype conferring competitive ability was irrespective of treatment. Future work should seek to understand how the spatial distribution of patches which vary in their quality may interact to influence intra-population growth variance and the real-world consequences of such variance for population regulation, potentially allowing for further insight as to the decisions, pressures and structuring factors which underlie patterns of individual distribution within natural landscapes.

CHAPTER II

POPULATION DENSITY AND NON-RANDOM PHENOTYPE-DEPENDENT HABITAT SORTING: THE CASE OF STREAM-FISHES

B. Jacobson, F. Dubois and P.R. Peres-Neto

Will be submitted to Oecologia

2.1 Summary

Landscapes are composed of heterogeneous habitats, the environmental conditions within varying spatially and/or temporally, influencing the distribution and phenotypic diversity of individuals both within and across populations. Such phenotype-habitat associations may arise either by individuals altering their phenotype to maximize fitness within their current environment (through plasticity or natural selection) or by keeping their phenotype but altering their habitat, using non-random movement and adaptive habitat matching. With respect to fish, polymorphisms are often studied within lakes whose stable environments allow for *in situ* adaptation; this mechanism potentially negated as an explanation for phenotypic sorting within temporally fluctuating streams where instead movement has been suggested to be particularly important. Here we set out to provide a test of non-random dispersal and phenotype-dependent habitat choice, investigating the degree to which this mechanism may influence the distribution of phenotypes between stream habitats as a function of intra-specific competition through the use of experimental trials manipulating density within an artificial stream, testing four stream-fish collected from either a single riffle or pool, as well as the development of a frequency-dependent game model. Contrary to expectation, individuals were found within both original and alternative habitats at low densities, however as expected the

degree of morphological differentiation between habitats decreased due to exclusion of comparatively less competitive (specialized) individuals from the use of optimal to sub-optimal habitats, these individuals potentially the mobile fraction of stream fish populations. The alternative habitat section used and degree of differentiation was found to be species dependent and based on swimming capacity, species most influenced by water velocity those with greater phenotypic sorting. Results were contrasted with predictions from the model which allowed individuals to vary in their preferences between two habitat types according to their growth rate, degree of interference, competition susceptibility and sampling capacity within each and established three contrasting patterns of phenotypic differentiation, no change, increased or decreased, as a function of density. According to the model, and upholding experimental findings, decreased differentiation with density requires that individuals with differing phenotypes have contrasting habitat preferences with only one phenotype dispersal-biased. Overall results from this study may help to account for the differential level of polymorphisms that are often found between stream and lake systems.

2.2 Introduction

Landscapes are composed of heterogeneous habitats, the environmental conditions within varying spatially and/or temporally, influencing the distribution and phenotypic diversity of individuals both within (small scale) and across (larger scale) populations. Indeed, as such, populations are known to be composed of individuals that vary in their morphological, behavioural or life history traits, differentially specialized for the use of a particular subset of the resources and/or environments utilized by the population as a whole (Bolnick *et al.*, 2003; Halama and Reznick, 2001; Skúlason and Smith, 1995; Smith and Skúlason, 1996; Wimberger, 1994). A variety of concepts have been put forward to explain how such phenotypic

heterogeneity, both within and across populations, is generated and maintained (coarse-fine-grain model by Levins, 1968; ecological specialization and trade-offs, see Futuyma and Moreno, 1988; adaptive *versus* non-adaptive phenotypic plasticity, see Ghalambor *et al.*, 2007), where several possibilities exist with respect to the way in which individuals attempt to maximize their fitness and phenotypes become correlated with different habitat conditions. Firstly, individuals may alter their phenotypes to better match their current habitats selective pressures, either occurring 1) within generations via physiological adjustments or behavioural flexibility or 2) across generations via natural selection (assuming trait heritability). Alternatively, individuals can instead 3) keep their phenotype but change the environmental conditions in which they are located (i.e., move or disperse, small or large scale respectively) (Edelaar *et al.*, 2008), termed phenotypic sorting or adaptive habitat matching.

With respect to fish, polymorphisms (i.e., phenotypic diversity) and the associated functional tradeoffs are often studied within lakes (see examples within Smith and Skúlason, 1996 and Wimberger, 1994) where individuals are sampled from, and are therefore *a priori* associated with either benthic or limnetic habitats (e.g., Bolnick, 2004; Robinson *et al.*, 1996; Schluter, 1995; Wilson, 1998). Here it is the second option, *in situ* adaptation (i.e., "classical local adaptation"; Edelaar and Bolnick, 2012), which is usually proposed to account for morphological differences. Indeed, there is extensive evidence showing that phenotypic variation within lake populations, which ranges from subtle to conspicuous morphotypes, is the product of disruptive selection, found to be afforded by the stable environmental conditions (Wimberger, 1994) and discrete resource distributions (Smith and Skúlason, 1996) provided between habitats (differential selective pressures of littoral *versus* pelagic) and driven by intra-specific competition; all phenotypes having similar fitness at low,

but only the most specialized phenotypes having high fitness at high densities (Bolnick, 2004; Svanbäck and Bolnick, 2007).

Strong species and phenotype-habitat associations, however, are also found within more temporally variable systems such as streams (Belica and Rahel, 2008; Lamouroux and Cattanéo, 2006; Schlosser, 1991); riffle species, for example, having streamlined fusiform morphology for increased swimming capacity *versus* pool species having laterally-compressed deeper bodies for increased maneuvering (Gatz, 1979; Leavy and Bonner, 2009). Here while such discrete habitat patches classified as pools, runs and riffles differ in water velocity, depth and substrate composition (Brown and Brussock, 1991; Lamouroux and Cattanéo, 2006; Rodríguez, 1995; Sagawa *et al.*, 2007), and thus also place very different selective pressures on the individuals within (Bolnick *et al.*, 2009), the temporally fluctuating environmental conditions (most notably water flow) and in association assemblage structure and population sizes found within streams (Palmer and Poff, 1997; Peres-Neto, 2004; Schlosser, 1991; Wimberger ,1994) potentially negates the possibility of the *in situ* adaptation found in lakes. Alternatively then, and recently gaining attention, non-random (directed) dispersal and phenotype-dependent habitat selection or phenotypic sorting (see Edelaar *et al.*, 2008 for a list of alternate terms) (option 3) may account for the phenotype-habitat associations found in streams. Indeed rather than being a source of maladapted individuals, which is often assumed, dispersal may instead increase the potential for local adaptation, individuals selecting the habitat which maximizes their fitness based on their phenotype (Armsworth and Roughgarden, 2005a, 2005b; Bolnick *et al.*, 2009; Bolnick and Otto, 2013; Edelaar and Bolnick, 2012; Edelaar *et al.*, 2008); movement and dispersal suggested to be particularly important in systems with high spatial and temporal heterogeneity (Armsworth and Roughgarden, 2005a; Edelaar *et al.*, 2008; Petty and Grossman, 2004). It is interesting to note that such an ability for individuals to phenotypically sort

themselves may differ as a function of the habitat with which they are associated, swimming ability found to be related to the water velocity in which the species (or individual) is found (Leavy and Bonner, 2009; Nelson *et al.*, 2003): pool species known to be impeded by the demands of intervening riffles (Lonzarich *et al.*, 2000; Schaefer, 2001), riffle species on the other hand potentially easily able to move through pools, having then a greater ability to sample available habitats.

In the present study, we set out to provide a test of non-random dispersal and phenotype-dependent habitat choice, as per Edelaar *et al.* (2008) and Edelaar and Bolnick (2012), and investigate the degree to which this mechanism may influence the distribution of individuals (phenotypes) between stream habitats across increasing levels of intra-specific competition (i.e., density). To do so, we conducted density trials within an experimental stream using four fish species collected (original habitat) from a single natural habitat section (pool or riffle), assessing the degree to which individuals selecting different habitat types within the artificial stream differed in their morphologies as a function of density. Here, as per habitat selection theory, we expected all individuals to be found within a single habitat section at low, but to increasingly utilize alternative habitats at greater densities (Fraser and Sise, 1980; Morris, 1988, 2003) and for this exclusion to alternative areas to be based on the relative competitive ability of an individuals phenotype within its original habitat. As water velocity is a large selective pressure within streams it was expected that swimming capacity, reflected in functional morphology, would play a large role in the distribution of phenotypes across habitat sections, species the most influenced by water flow being those with greater phenotypic sorting. The results from these experiments were contrasted with the predictions from a frequency-dependent (game) model in which individuals were allowed to vary in their preferences between two habitat types according to four parameters: growth rate, degree of interference, competition susceptibility and sampling capacity within each of the two habitat types.

By varying model parameters, three contrasting patterns of the degree of phenotypic differentiation between the two habitats as a function of density were established: no change or increased or decreased phenotypic differentiation. The experimental trials found phenotypic differentiation between individuals in different habitat sections to decrease as density increased where according to our model this pattern requires that individuals with different phenotypes have contrasting habitat preferences and movement is biased in relation to only one phenotype. Overall results from this study may help to account for the differential level of polymorphisms that are often found between stream and lake systems.

2.3 Experimental trials

2.3.1 Materials and methods

2.3.1.1 Species collection and artificial stream set-up

Two riffle species, blacknose dace (*Rhinichthys atratulus*) and mottled sculpin (*Cottus bairdi*) and two pool species, creek chub (*Semotilus atromaculatus*) and johnny darter (*Etheostoma nigrum*) (Figure 1.1A) (Bernatchez and Giroux, 2000) were collected from either a single riffle or pool (referred to throughout as original habitat) from separate streams by way of upstream single-pass zigzag backpack electrofishing (Smith-Root Inc.). Species were selected so that one species from each habitat type was mid-water column and one benthic in order to capture potential differences in sampling and competitive ability. Individuals were transported to the Penfield Nature Reserve in Austin, QC, Canada where experiments were conducted. When not in use, fish were housed within 300 gallon tanks, with water $^{3}/_{4}$ exchanged daily to help control temperature and quality, kept on a 12:12hr light: dark cycle (lights on 7am) and fed frozen brine shrimp *ad libitum* twice daily.

Experiments were conducted within an artificial stream comprised of four habitat sections with pool, riffle and two run sections set-up to mimic, as much as possible, natural conditions (Figure 2.1B). The riffle (width: 41.9cm, length: 264.2cm, depth: 49.5cm) was composed of large rock-boulder substrate as well as 4 submersible water pumps to increase water velocity above that of surrounding sections, velocity averaging 8.52m^3/h (average of 12 measurements, range 5.33- 21.74m^3/h). The pool section (width: 128.3cm, length: 264.2cm, depth: 76.2cm) was filled with a 2 sand:1 gravel mixture, contained submerged wood piles and had an average water velocity of 5.33m^3/h. Lastly, both runs (width: 41.9cm, total length: 421.6cm, depth: 49.5cm) were lined with gravel and dotted with medium pebbles with an average velocity of 7.06m^3/h. Note that in order to help control water temperature a $^1/_3$ HP chiller (Frigid Units,) set to 22°C was installed in one of the runs which increased its water velocity slightly.

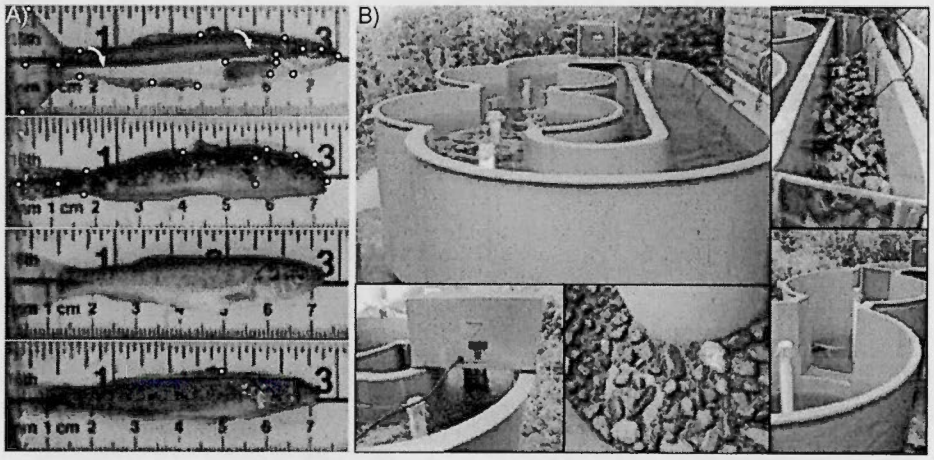

Figure 2.1. Four species tested, morphological landmarks and artificial stream. A) Species tested in order from top to bottom: blacknose dace (mid-water column), mottled sculpin (benthic), creek chub (mid-water column) and johnny darter (benthic). Morphometric landmarks for mid-water column and benthic species are the same, arrows denote the location of body and caudal peduncle width caliper measurements. B) Artificial stream containing riffle (inset top right), pool (inset bottom right) and two curved run sections.

2.3.1.2 Experimental procedure and data analysis

All experiments were conducted with a single species (intra-specific considerations) at a time. Two days prior to the start of density trials individuals were anesthetized using a 1 clove oil:10 ethanol mixture (active agent eugenol) (Keene *et al.*, 1998; Munday and Wilson, 1997) and given a unique combination of 2 subcutaneous VIE tags (visible implant elastomer; Northwest Marine Technologies) by way of 4 fluorescent colours and several body locations. No mortality was observed due to handling procedure and no differential mortality or trial outcomes were noted to occur as a result of either tag colour or location. While anesthetized, individuals were photographed on one lateral side for morphology, their fork length was recorded and their body and caudal peduncle widths were measured using calipers (Figure 2.1A). In order to transform photographs into morphological information geometric morphometrics were used, landmarks added (Figure 2.1A) using the program tpsDIG2 (Rohlf, 2005a).

Experiments within the artificial stream were conducted continuously from July 11 to August 26 2009, with each trial running from 10am one day to 7am the next. Individuals participating within a trial were randomly selected from the holding tank (after ensuring non-consecutive trial participation), separated into 4 equal groups and released into blocked off habitat sections. Blockades were afterwards simultaneously removed allowing individuals to swim freely throughout the system, which was covered with mosquito screen to prevent individuals from jumping. At 7am the following day, blockades were re-established and individuals found within the separate sections were captured and identified based on their unique tag. Three hours were left between the end and start of trials to allow time for recapture and the exchange of all water within the system.

2.3.1.2.1 Density effects and morphological analysis

In order to test the effect of density on habitat use four density levels were tested: ½D, D, 2D and 3D where D (density) was based on an estimation of approximate individual abundance at the time of species collection. For riffle species D was set at 20, a range of 10-60 individuals tested, while for pool species D was set at 30, testing a range of 15-90 individuals. The order in which density levels were tested was randomly determined and each level was replicated once. Note that due to several instances of either chiller related mortality or an inability to recapture individuals within the 3-hour time-frame, final densities did not always match initially set levels (see Table 2.1).

To determine the influence of morphology for individual habitat selection, landmarks for the individuals participating in each trial were converted into partial warp scores (shape variables) using the programs Coordgen6 and PCAgen6 (Sheets, 2004a, 2004b). Partial warp scores were then entered within a principal component analysis (PCA) and all possible resultant factors used within a forward selection discriminant function analysis (DFA), individuals differentially coded based on in which of the 4 habitat sections they were found. In order to visualize any morphological differences between individuals occupying original versus alternative habitats across densities, deformation grids were produced using the program tpsRegr (Rohlf, 2005b). To insure that any morphological discrepancies between trials were not the product of the random sample of participating morphologies (i.e., low density trials did not contain a non-random subset of the morphologies within high density trials), partial warp scores were produced for all individuals tested across trials and used within a PCA and then DFA with individuals coded based on trial participation. Lastly, as fish competitive ability is often linked to size (Ward *et al.*, 2006; Young *et al.*, 2004) and within geometric morphometrics this effect is removed through standardization

(Zelditch *et al.*, 2004), univariate analyses of variances (ANOVAs) were conducted for each trial to test the potential influence of $\log_{10}$ transformed fork length, body and caudal peduncle widths for the differential selection of habitat sections.

2.3.1.2.2 Habitat manipulations

To determine the importance of the differentiating habitat properties between pools, runs and riffles (i.e., water depth, velocity or substrate) for habitat selection, three un-replicated habitat manipulations were performed for each species using the density D after the conclusion of density trials. Each manipulation systematically altered the species original habitat type to take on properties of the extreme opposite (i.e., pool changed to riffle, riffle to pool) either: (1) pumps removed from the riffle or added to the pool; (2) boulders replaced by sand in the riffle or sand replaced by boulders in the pool; and (3) both velocity and substrate (manipulations 1 and 2) altered together.

In order to determine the impact of such manipulations for habitat selection contingency table analyses were performed, comparing the average distribution of individuals in original versus alternative habitats found within D density trials with habitat use from manipulations. Partial warp scores, PCAs and DFAs were computed as within density trials to determine the influence of morphology for habitat use, and univariate ANOVAs were run to test for the influence of fish size. All PCAs, DFAs, ANOVAs and contingency table analyses were performed using Statistica 6.0 (StatSoft).

2.3.2 Results

2.3.2.1 Density effects

All trials conformed to random morphological sampling, results from the DFA showing no morphological distinction between trials (blacknose dace: Wilks' Lambda=0.540, $F(224, 1492)=0.627$, $p<1.000$; mottled sculpin: Wilks' Lambda= 0.743, $F(126, 1547)=0.568$, $p<1.000$; creek chub: Wilks' Lambda=0.634, $F(224,2308)=0.710$, $p<1.000$; johnny darter: Wilks' Lambda=0.678, $F(140, 2375)=1.022$, $p<0.4158$). Note that while all experiments were conducted for each of the 4 species, results following from those of creek chub will not be presented, individuals of this species found to shoal (Fraser and Sise, 1980, Magnan and FitzGerald, 1984) and thus not conform to assumptions of habitat selection (Morris, 2003). For the remaining three species, across all densities tested, individuals were found within both original and alternative habitats, the number of individuals found in and the number of alternative sections used increasing as densities increased (Figure 2.2A; Table 2.1). The alternative habitat section predominately used across densities was species dependent, blacknose dace (riffle, mid-water column) using run, mottled sculpin (riffle, benthic) using marginally more pool than run, and johnny darter (pool, benthic) using riffle sections.

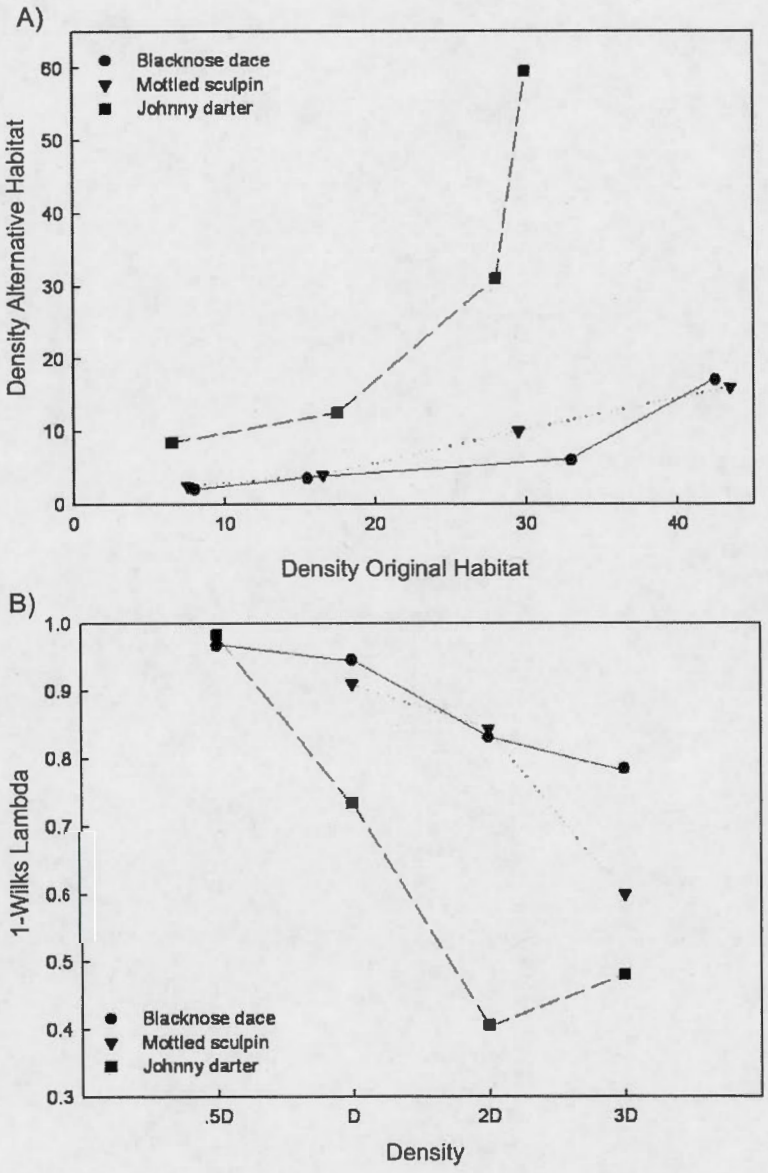

Figure 2.2. Habitat selection and morphological discrimination outcomes of density trials. Points represent the average of replicates per density level. A) Graph showing habitat section use across densities. Alternative habitat denotes the cumulative number of individuals in the 3 non-original habitat sections. B) Graph of the degree of morphological distinction between individuals selecting different habitat sections from DFAs. Note when only a single DFA could be conducted per density level, point is not averaged.

Table 2.1. Habitat selection and morphological discrimination outcomes of density trials. Original is riffle for the first two species and pool for the last, Alternative refers to the cumulative number of individuals in the remaining three habitat sections, n is the number of these sections utilized and morphology the degree of discrimination (1-Wilks' lambda) based on DFAs. All morphology is significant at $p \leq 0.05$ except for the value in italics.

Density	Replicate	Blacknose dace			Mottled sculpin			Johnny darter		
		Original	Alt. (n)	Morphology	Original	Alt. (n)	Morphology	Original	Alt. (n)	Morphology
.5D	1	7	3 (1)	0.967	8	2 (2)	----	10	5 (1)	0.98
	2	9	1	----	7	3 (3)	----	3	12 (2)	0.987
D	1	17	2 (1)	0.997	14	6 (2)	0.911	21	9 (2)	0.591
	2	14	5 (1)	0.894	19	2 (2)	----	14	16 (3)	0.878
2D	1	29	9 (3)	0.85	27	12 (3)	0.79	33	26 (2)	0.458
	2	37	3 (1)	0.803	32	8 (3)	0.896	23	36 (3)	*0.354*
3D	1	27	32 (3)	0.784	48	11 (3)	0.743	33	57 (3)	0.453
	2	58	2 (2)	----	39	21 (3)	0.453	27	62 (2)	0.507

Such patterns of habitat use were not the product of competitive ability conferred through size, ANOVAs of the relationships between habitat use and fork length, body and caudal widths overall largely non-significant (Table 2.2). Instead habitat selection was found to be morphologically dependent, results from DFAs showing the morphologies of individuals found in different habitat sections to always be significantly differentiated, though the degree of such differentiation decreased as densities increased (Figure 2.2B; Table 2.1); 3D for johnny darter was the sole exception, more differentiated than 2D. This overall pattern could also be seen within deformation grids (e.g., Figure 2.3: within density levels) where at low densities individuals within original versus alternative habitats were those with higher placed eyes, shorter pectoral fins, deeper caudal fork and larger head and caudal fin for blacknose dace, larger head, body and wider pectoral fins for mottled sculpin and slender body, lower placed eyes and pectoral fins for johnny darter; such differences averaging at higher densities. This averaging was found to be the product of competitive exclusion of morphologies adapted to original habitat to the use of alternatives at such higher densities. For example, for blacknose dace (Figure 2.3:

across density levels), morphologies of individuals in original habitat were not greatly differentiated between low and high densities whereas individuals in alternative habitats at higher densities had higher placed eyes and larger heads and caudal fins (as per original habitats) compared to low densities. Note that while blacknose dace was overall the most differentiated species across densities this was not the by-product of the greater number of landmarks used to capture its morphology, patterns within Figure 2.2B not changed with the use of a reduced set of landmarks (*results not shown*).

Table 2.2. F-values from univariate ANOVAs of the influence of length, body and caudal width for habitat selection. Numbers in brackets are the degrees of freedom within tests of that replicate.

Density	Replicate	Blacknose dace			Mottled sculpin			Johnny darter		
		Length	BodyW	CaudalW	Length	BodyW	CaudalW	Length	BodyW	CaudalW
.5D	1	2.800 (1)	0.083	1.100	1.638 (2)	2.044	1.100	8.279* (1)	6.111*	2.340
	2	0.051 (1)	0.954	0.485	1.521 (3)	1.476	0.065	4.437* (2)	0.707	3.101
D	1	2.887 (1)	0.051	0.124	1.692 (2)	1.168	0.855	0.200 (2)	0.055	0.424
	2	9.886* (1)	6.008*	5.069*	0.193 (2)	0.072	1.951	2.805 (3)	2.949	0.689
2D	1	3.873* (3)	0.282	6.128*	5.482* (3)	4.880*	3.596*	0.651 (2)	0.796	0.031
	2	1.599 (1)	0.080	0.086	1.449 (3)	0.944	0.863	0.512 (3)	0.641	0.266
3D	1	3.163* (3)	1.011	3.013*	3.159* (3)	2.289	2.065	9.272** (3)	6.018**	1.124
	2	0.485 (2)	0.268	2.520	1.287 (3)	0.912	1.289	6.748* (2)	4.582*	1.275
	Velocity	0.454 (1)	0.368	6.258*	1.466 (2)	1.258	2.398	0.389 (3)	0.650	0.731
	Substrate	6.494* (2)	7.143*	2.832	0.592 (1)	0.888	1.088	1.354 (3)	0.709	0.264
	Both	5.763* (1)	7.406*	4.046	7.863* (1)	10.590*	6.464*	2.253 (3)	1.878	2.876

p≤0.05*
p≤0.001**

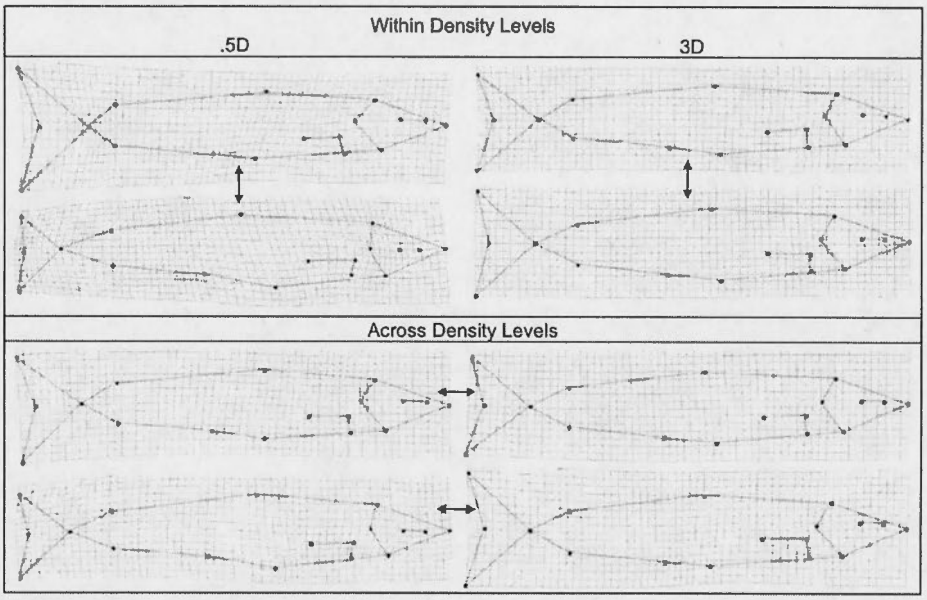

Figure 2.3. Representative deformation grids of blacknose dace showing relative morphological variation within and across density levels between individuals selecting original versus alternative habitat sections. For each section top grid is original and bottom alternative habitat, visualization is 3x relative differences.

2.3.2.2 Habitat manipulations

As evidenced from contingency table analyses (Table 2.3), the habitat manipulations conducted had a variable impact on habitat selection, ranging from no change in habitat use compared to that within D density trials for blacknose dace to a complete switch in habitat selection for mottled sculpin, individuals using pools over original habitat for all manipulations. For johnny darter, only when pumps were added to the pool without the change of substrate did individuals change their habitat selection, using predominantly riffles. As within density trials, as per DFAs (Table 2.3) and ANOVAs (Table 2.2) habitat selection was morphologically, and not size, dependent.

Table 2.3. Outcomes of habitat manipulations and resultant morphological considerations. Original is riffle for the first two species and pool for the last, Alternative refers to the cumulative number of individuals in remaining three habitat sections, n is the number of these sections utilized. $\chi 2$ is the result of contingency table analysis, morphology the degree of discrimination (1-Wilks' lambda) based on DFAs.

Species	Manipulation	Habitat selected		χ^2	Morphology
		Original	Alt. (n)		
Blacknose dace	Velocity	13	7 (1)	1.13	0.958**
	Substrate	12	8 (2)	1.90	0.975**
	Both	15	4 (1)	0.01	0.848*
Mottled sculpin	Velocity	6	14 (2)	10.10**	0.990**
	Substrate	1	19 (1)	23.02**	----
	Both	1	19 (1)	23.02**	----
Johnny darter	Velocity	10	19 (3)	3.40*	0.765**
	Substrate	14	16 (1)	0.85	0.986**
	Both	18	12 (3)	0.01	0.821*

* $0.05 \leq p \leq 0.10$
** $p \leq 0.05$

2.4 Frequency-dependent game model

2.4.1 Model outline

We assume that individuals of a population of N competitors can be of two phenotypes (i.e., phenotype A and B), where x and $(1-x)$ denote the relative proportion of each phenotype, respectively. Individuals can choose between two habitats (i.e., habitat 1 and 2) that differ in their characteristics. The two phenotypes may have distinct morphologies, and for the sake of simplicity, morphological traits of each phenotype are represented by a single value V_A and V_B for phenotype A and phenotype B individuals, respectively, with $V_A=1$ and $V_B=2$. Such morphological differences can be associated with different expected levels of fitness in the two habitats with the growth rate (i.e., fitness) of phenotype A denoted as λ_{A1} and λ_{A2} in

habitats 1 and 2, and the fitness of phenotype B in each habitat as λ_{B1} and λ_{B2} (with $\lambda_{A1}+\lambda_{A2}=1$ and $\lambda_{B1}+\lambda_{B2}=1$). We assume that individuals of phenotype A have a greater growth rate in habitat 1 than in habitat 2 (i.e., $\lambda_{A1}>0.5$), and, conversely, that phenotype B individuals may prefer either one or the other habitat.

Following assumptions of density-dependence, individual growth rate decreases as the number of competitors increases within the habitat (Morris, 1987, 2003) due to interference competition, where the degree of interference may vary between the two habitats due to quantitative and/or qualitative differences (*sensu* Morris, 1988); α_1 and α_2 denote the degree of interference for habitats 1 and 2, respectively. The influence of this parameter is considered to vary depending on the competitive ability of individuals which, contrary to ideal-free assumptions (Abrahams, 1986; Kennedy and Gray, 1993), differs amongst individuals where each phenotype is characterized by a measure of its susceptibility to competition (C_A and C_B for phenotypes A and B) reflecting the degree to which it is affected by (i.e., expected fitness is reduced) the presence of competitors. Differences in competition susceptibility between the two phenotypes are likely to be related to some aspects of their morphology, such as their body shape, mass or size. Similarly, we assume that phenotypes differ, due to morphology, in their ability to sample the environment (i.e., vary in speed of or cost incurred when moving between habitats) where both phenotypes are able to perfectly estimate their expected fitness within their preferred habitat, but either over- or underestimate fitness within their sub-optimal habitat. This bias is ε_A and ε_B for phenotype A and phenotype B individuals, respectively and also counters the ideal-free assumption of perfect system knowledge (i.e., sampling; see Abrahams, 1986; Kennedy and Gray, 1993).

To estimate the proportion of both phenotypes in habitats 1 and 2, simulations are run for N steps (i.e., population size) where both habitats are empty at the beginning of a

simulation and individuals are then introduced, one at each step, and decide which habitat to occupy based on their estimate of expected fitness. The expected fitness depends on their real or assessed performance within the two habitats given their phenotype, as well as on the number of competitors already present within each (n_1 and n_2 for habitats 1 and 2, respectively) when they make their decision. For instance, the expected fitness of a newly introduced individual of phenotype A is $\hat{W}_{A1}$ and $\hat{W}_{A2}$, in habitats 1 and 2, with:

$$\hat{W}_{A1} = \lambda_{A1} - \alpha_1 \times C_A \times n_1$$

and

$$\hat{W}_{A2} = \lambda_{A2} + \varepsilon_A - \alpha_2 \times C_A \times n_2$$

Based on its estimation of expected fitness, the individual decides to settle in habitat 1 if $\hat{W}_{A1} > \hat{W}_{A2}$ or otherwise in habitat 2. At each step, the phenotype of a newly introduced individual is chosen randomly, unless all individuals of a particular phenotype have already been introduced, in which case all subsequent introduced individuals are necessarily of the alternative phenotype. Given that the decision of individuals to settle or not in their *a priori* optimal habitat is strongly contingent on the order at which they are introduced in the environment, we ran the simulation 10 000 consecutive times for a given set of parameter values and we estimated from these 10 000 repetitions the mean proportion of phenotype A individuals in habitats 1 and 2 (i.e., p and 1-p) as well as the mean proportion of phenotype B individuals in habitats 1 and 2 (i.e., q and 1-q). From these probabilities, we calculated the mean morphological value of individuals within the two habitats (i.e., V_1 and V_2 in habitats 1 and 2, respectively) as:

$$V_1 = \frac{pV_A + qV_B}{p+q}$$

and

$$V_2 = \frac{(1-p)\times V_A + (1-q)\times V_B}{(1-p)+(1-q)}$$

The absolute difference between these values $|V1-V2|$ was then used as an index of morphological dissimilarity between the two habitats. Small differences reflect situations where there is an equivalent proportion of A and B phenotypes in each habitat. Conversely, the difference is maximal when phenotype A individuals mainly occupy one habitat while phenotype B individuals mainly choose the other. Here we set x=0.5 and tested all combinations of parameter values using the ranges N=10 to 150 , λ_{A1}= 0.5 to 1, λ_{B1}=0 to 1, α=0 to 1, C=0 to 1 and ε=-1 to 1, N varied at increments of 10, all other parameters at 0.1, using C++.

2.4.2 Model results

By varying model parameters (i.e., growth rate, degree of interference, competition susceptibility and sampling capacity), three main contrasting patterns in terms of the degree of phenotypic differentiation between the two habitats as a function of density were established (Figure 2.4A and B: no change, Figure 2.4C and D: increased or Figure 2.4E and F: decreased phenotypic differences). As expected from habitat selection theory, the model predicts that the proportion of individuals that settle in their sub-optimal habitat increases with density (Figure 2.4A, C, E). However, increasing population size (i.e., density) has different effects on the mean level of phenotypic dissimilarity between the two habitats, depending both on the growth rate of each phenotype in each of the habitats, as well as on whether individuals from both

or just one of the phenotypes is likely to disperse into their sub-optimal habitat. More precisely, if there is no bias in dispersal, the absolute difference between the average trait value of the two habitats remains constant regardless of N, the proportion of individuals of phenotype A and B using sub-optimal habitats equivalent (Figure 2.4B). Such a situation arises, for instance, when morphological differences do not correlate with differences in growth rate, competitive ability or sampling capacity: at low competitor densities, all individuals occupy their preferred habitat and then tend to disperse as competition becomes more intense, irrespective of their phenotype.

Conversely, when one phenotype is more likely to use its sub-optimal habitat than the other (i.e., is dispersal-biased), then the phenotypic dissimilarity between the two habitats either increases or decreases as N increases (Figure 2.4D and F). Such phenotypic dissimilarity between the two habitats tends to increase with density when individuals have the same initial habitat preference so that both A and B phenotypes select the same habitat at low densities but here only individuals from one phenotype disperse to the sub-optimal habitat when competition intensity increases (Figure 2.4D). Such a bias can result from individual differences in i) growth rate (the dispersing phenotype that with the lowest growth rate in the optimal habitat), ii) sampling ability (the dispersing phenotype that with the lowest assessed performance in the optimal habitat), or finally iii) competitive capacity (the dispersing phenotype that more affected by competition). Alternatively, the phenotypic dissimilarity between the two habitats instead decreases with increasing competition when phenotypes A and B are each best adapted to a different habitat: at low densities, the two habitats are each occupied by only one phenotype and hence are very dissimilar (Figure 2.4E). As competition increases, only one phenotype disperses into its sub-optimal habitat (Figure 2.4E), thereby shifting the average trait value within towards that of the dispersing phenotype, leading to a decrease in the absolute difference between the two habitats (Figure 2.4F).

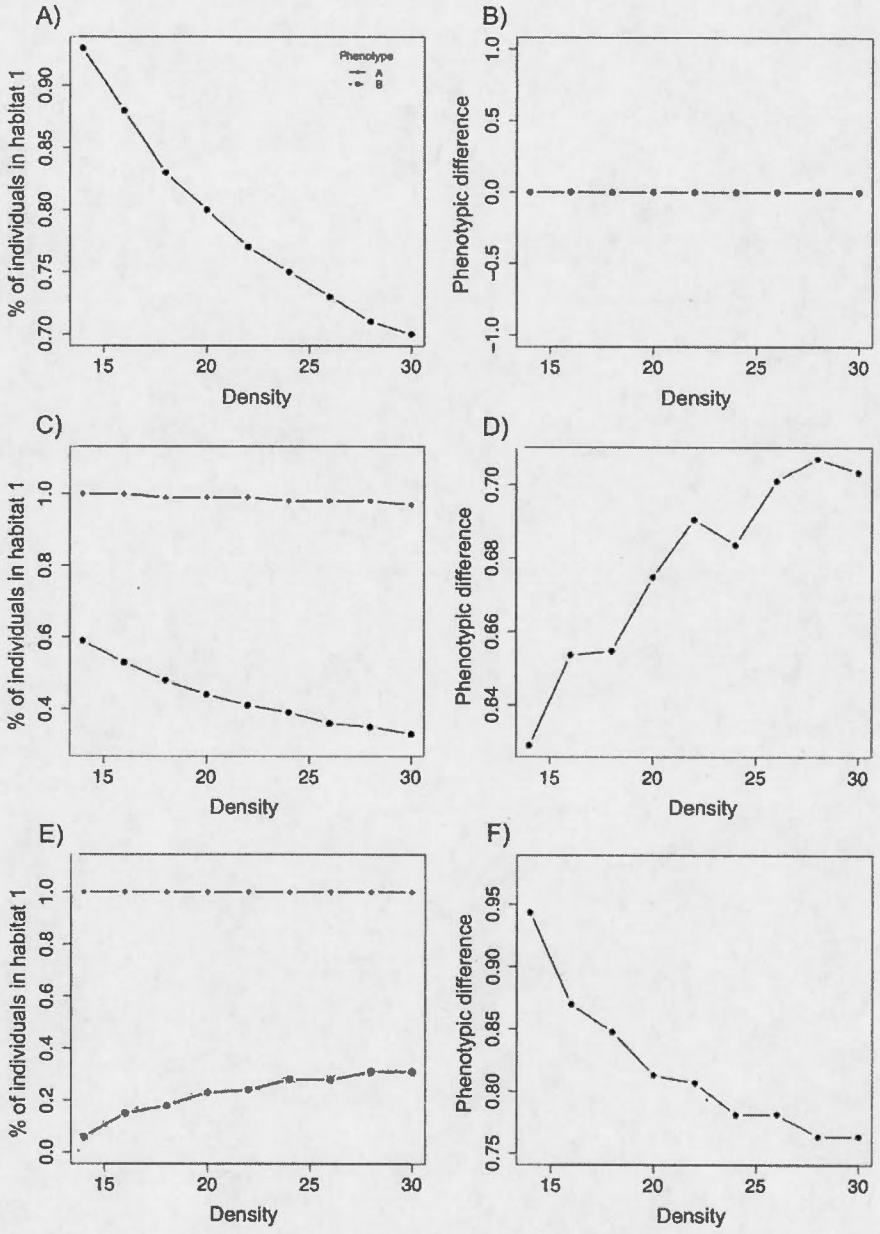

Figure 2.4. Effects of population density on: i) the expected proportion of both phenotypes in habitat 1 (panels A, C, E) and ii) the absolute difference in the mean trait between the two habitats (panels B, D, F). In all panels: λ_{A1}=0.8, C_A=1, C_B=1 and α_1=0.1 and ε_A=0.0. In panels A and B: λ_{B1}=0.8, α_2=0.1 and ε_B=0.0; in panels C and D: λ_{B1}=0.4, α_2=0.1 and ε_B=0.5; in panels E and F: λ_{B1}=0.2, α_2=0.3 and ε_B=0.0.

2.5 Discussion

2.5.1 Generalities: influence of morphology for habitat selection

While, as expected, individuals were found to increasingly utilize non-original habitat sections as density increased, intra-specific competition known to lead to niche expansion (Araújo *et al.*, 2008; Bolnick *et al.*, 2003; Svanbäck and Bolnick, 2007), here such non-original habitat use also occurred at even the lowest densities tested. That this differential habitat selection at such low densities was associated with a large degree of morphological distinction between individuals in the different habitat types, morphologies functionally adapted to the environments selected (see 2.5.2 Species specifics below), points to the action of adaptive habitat matching (Bolnick *et al.*, 2009; Edelaar and Bolnick, 2012; Edelaar *et al.*, 2008), especially since habitat choice at this density was independent of the potential effects of competition (Edelaar *et al.*, 2008). Given that within this study individuals were collected from a single stream habitat section, this suggests that a proportion of the individuals found within the section were actually best adapted for use of an alternative (this also confirmed by our model predictions, see below); their relegation to the environment in which they were collected potentially due to restriction by the presence of other species (Bolnick *et al.*, 2003; Rodríguez, 1995; Smith and Skúlason, 1996; Wimberger, 1994) and/or high densities of conspecifics within their optimal alternative.

The use of phenotype-dependent habitat selection, as predicted, also occurred at higher densities, the degree of morphological differentiation between individuals occupying differential habitat sections found to decrease, but still significant. Results from the deformation grids show that such decreasing differentiation was the product of individuals otherwise adapted for the use of original sections instead excluded to alternatives. This was likely due to increased intra-group competition within the

habitat sections (Araújo *et al.*, 2008), individuals less competitive (i.e., comparatively less adapted) leaving, while those more specialized able to remain at high system densities; akin to a lake-stream transplant study by Bolnick *et al.* (2009) which found stream individuals remaining in lakes to have comparatively more lake-like morphology than those who returned to the stream. Such specialized individuals, those the most adapted to the environment that they occupy, then, may be able to remain stationary across densities (see 2.5.3 Conclusions below). As populations of many stream fish are known to be composed of a fraction that is stationary and a (smaller) fraction that is mobile (Belica and Rahel, 2008; Fraser and Sise, 1980; Lonzarich *et al.*, 2000; Petty and Grossman, 2004; Rodríguez, 2002; Skalski and Gilliam, 2000), it is perhaps these mobile individuals which are excluded at higher system densities, having less specialized phenotypes since morphology is not only shaped by the habitat within which individuals are found but also through which they move and are exposed (Morris, 2003; Nelson *et al.*, 2003; Schaefer, 2001).

Supporting these experimental results, one important prediction of the model was that the dissimilarity (morphological differentiation) between the two habitats was expected to either increase or decrease with density when only one phenotype was dispersal-biased, the direction of differentiation depending on whether the two phenotypes preferred the same or different habitats. According to the model, decreasing morphological differentiation between habitats as a function of density should occur when phenotypes within the system are differently adapted to the use of, and thus prefer, different habitats and it is exactly these conditions which were found from experimental trials. Indeed individuals, while all sampled from the same original habitat, were found to occupy both original and alternative habitat types as a function of their morphology, with individuals utilizing original habitats at low densities those that were perhaps under the greatest competitor pressures and thus dispersing to the use of alternatives (i.e., sub-optimal) (akin to phenotype B in Figure

2.4E), individuals within alternative sections at low densities not dispersing (no dispersal bias) at higher densities both due to potentially lower competitor pressures as well as an inability due to swimming capacity.

2.5.2 Species specifics: individual and habitat properties for section use

While all three species showed the same general pattern of phenotype-dependent habitat use across densities, the habitat sections utilized and degree of distinction, as expected, differed between species as a function of their swimming propensity/capacity (water-column *versus* benthic); reflected in the functional morphological adaptations found within original versus alternative habitat sections as per deformation grids. Indeed the mid-water column species, blacknose dace, utilized runs as the predominate alternative section, the relative morphology of individuals within riffles, who had shorter pectoral fins and a larger deeper forked caudal fin, reflecting a greater swimming capacity within such high water velocity (Gatz, 1979; Leavy and Bonner, 2009; Peres-Neto and Magnan, 2004). This species likely remained the most differentiated across densities due to the specific morphological properties required for individuals to efficiently use the energetically demanding riffle (i.e., run individuals not capable of efficiently utilizing the riffle), habitat manipulations not altering the distribution of individuals since they are already adapted to the most demanding environment. Note that such an influence of water velocity on the use of habitats by mid-water column species may have in fact increased the shoaling tendency that was found with respect to the mid-water colum pool species creek chub.

In contrast both benthic species, mottled sculpin originating from riffle and johnny darter from pool habitats, were less influenced by energetic constraints (Facey and

Grossman, 1992), phenotypes thus potentially more interchangeable amongst habitats, morphologies here found to be less differentiated across densities with habitat use related to diminishing velocity exposure. Indeed mottled sculpin used pools and johnny darter the riffle as alternative habitats instead of intermediate velocity runs, potentially due to an inability to hold station in runs where velocity isn't buffered by rocks (Jackson *et al.*, 2001) as it is in the riffle; the wider pectoral fins (Facey and Grossman, 1992; Webb *et al.*, 1996) for sculpin and deeper body (Guill *et al.*, 2003) for darter individuals found within riffles associated with the use of this habitat. Responses to habitat manipulations also reflected such habitat associations where johnny darters used riffles in the face of unbuffered velocity within pools and mottled sculpin used pools in the face of all manipulations; here pointing to both the need for buffered velocity for the use of riffles and a preference for deeper water (outcome of manipulations 1 and 3), this species known to seek shelter (Facey and Grossman, 1992). Note that johnny darter was the only species found to be more differentiated at the highest density tested, this potentially due to a saturation of space within pools, almost the same number of individuals utilizing pools in 2D and 3D, individuals found to burrow within the substrate (*personal observation*) as a way to shelter themselves from predators (Page and Swofford, 1984).

2.5.3 Evolutionary and ecological conclusions

Results from this study show the ability for stream-fish to use adaptive habitat matching, thus accounting for the phenotypic sorting and phenotype-habitat correlations found within such temporally variable systems. That here, as per both experimental and model outcomes, phenotypic sorting at higher densities acts through exclusion of individuals from their original to alternative habitats (preferred to sub-optimal) based on relative competitive abilities (i.e., specialized versus more

generalist morphologies), potentially accounts for the different degrees of polymorphism that can/has been found within lake versus stream systems. Indeed, as mentioned previously, morphological variation between individuals within lake populations can range from subtle, only detectable with the use of multivariate statistics, to conspicuous morphotypes that can be easily visually differentiated (e.g., stickleback) (Robinson *et al.*, 1996; Wilson, 1998). For species that distribute themselves across benthic and limnetic habitats irrespective of density it is the latter case which has the potential to develop (through disruptive selection; Bolnick, 2004), both specialist and generalist phenotypes having been found to consistantly associate with a particular habitat (Wilson, 1998), thus always facing selective pressures in the same direction; less variation is found for species that instead utilize a single habitat at low, but multiple habitats at high densities and thus face differing selective pressures (see Svanbäck and Persson, 2009). It is this latter situation that is found in streams where the degree of polymorphic variation between individuals is small, though still ecologically significant, and we found differing habitat associations of comparatively more generalist phenotypes as a function of density (e.g., able to use the riffle at low but excluded to run at high densities for blacknose dace).

The movement between habitat sections of comparitively generalist phenotypes may be an attempt of such individuals to maximize their fitness in the face of increased competitor pressure, some evidence, albeit variable, suggesting that the mobile fraction of adult fish populations may have lower fitness (growth) than the stationary fraction (Petty and Grossman, 2004; Skalski and Gilliam, 2000). As it may be questioned whether such growth differences are in fact the cause or the consequence of movement, future studies should test for the potential for increased individual fitness as a function of phenotype-dependent habitat selection (element 4 in Edelaar *et al.*, 2008).

CHAPTER III

THE TEMPORAL TRAJECTORY OF COMMUNITY TRAIT RE-ASSEMBLY: MORPHOLOGICAL TRENDS AS A FUNCTION OF HABITAT

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Will be submitted to Oikos

3.1 Summary

Community ecologists have long investigated patterns of community structure, interested in the process of, and mechanisms driving, community assembly, notable early studies attempting to define assembly rules and focusing on species pairs, identities and the role of competition. Recently there has been a renewed interest in the use of trait-based ecology, allowing results to be generalized beyond the species pool studied and a functional understanding of the relationship between community structure and environmental conditions. To date community assembly studies can be classified as belonging to one of two complementary, but not as yet integrated, groups. The first, trait-based studies, use metrics and null models to investigate the relative influence of habitat filtering and competition for community structure, though here the process of assembly is not followed, snap-shot observational data used. The second group explores the process of assembly, investigating whether communities follow deterministic or stochastic trajectories, though still largely focuses on compositional changes. The goal of this study, then, was to bridge the gap between these two groups of literature and follow the trajectory of trait-based community assembly, investigating how both overall and within-community trait relationships vary temporally and as a function of environmental selectivity. To do so we performed a defaunation experiment within a stream reach and followed the

natural fish re-colonization of habitat sites, analyses conducted using all the entire stream community and each of the two most abundant species. As expected, morphologies within different habitat types were significantly differentiated, indicating habitat filtering, and followed a deterministic trajectory towards pre-defaunation states. With respect to within community trait interactions, average distance and average NND metrics again indicated a greater role of habitat filtering over competition, where riffle and run communities were more deterministic through time than those in pools. Findings from this study and comparisons between community and component species temporal patterns provide a more detailed understanding of community structure and represent a potential next step in analyses of the process of community assembly.

3.2 Introduction

Community ecologists have long investigated patterns of community structure, interested in the process of, and the underlying mechanisms driving, community assembly. Notable early studies, such as Diamond (1975), searched for and attempted to define assembly rules, investigating the compatibility of species pairs and focusing on the role of competition in structuring ecological communities. Not long afterward, Connor and Simberloff (1979) advocated for the need to test potential structure and proposed mechanisms against a null hypothesis to assure that species distributions within and across local communities were in fact different from what might be expected by chance. While such studies greatly advanced community ecology, their use of species identities (and pairs) resulted in findings being highly contingent on the species pool and location studied (McGill *et al.*, 2006; Weiher and Keddy, 1995), the field criticized as a collection of case studies (Lawton, 1999; Simberloff, 2004). In order to address this issue of generalization, perhaps starting with Fox (1987), recently there has been a renewed interest in and call for a more trait-based ecology

and the use of functional traits rather than species identities, traits allowing for both results that can be generalized beyond the particulars of the study, as well as a functional understanding of community structure and its link with the environmental conditions within which the community is found (Frimpong and Angermeier, 2010; McGill *et al.*, 2006; Messier *et al.*, 2010; Weiher and Keddy, 1995).

To date, studies of community assembly can be classified as belonging to one of two complementary, but not as yet integrated, groups. The first, and that which is currently at the forefront, are exactly studies of trait-based community structure and assembly, investigating the degree to which communities are structured by two assembly mechanisms: environmental/habitat filtering which leads to community trait under-dispersion and/or limiting similarity (i.e., niche differentiation, competition) associated with trait over-dispersion (Cornwell *et al.*, 2006; Weiher *et al.*, 2011; Weiher and Keddy, 1995, 1999). Here community-level metrics are calculated to test for each potential mechanism, trait range and variance (univariate) or volume (multivariate) for filtering, nearest neighbour distance (NND) for limiting similarity, and compared to a null model (e.g., Ackerly and Cornwell, 2007; Ingram and Shurin, 2009; Kraft *et al.*, 2008; Kraft and Ackerly, 2010; Weiher *et al.*, 1998); where community structure has been found to differ along environmental gradients (e.g., Cornwell and Ackerly, 2009), greater under-dispersion expected under harsh abiotic conditions (Fukami and Lee, 2006). While such studies, primarily use species-level trait means, interested in inter-specific interactions, the potential importance and structuring role of intra-specific variation has started to gain attention (Albert *et al.*, 2010a, 2010b; Bolnick *et al.*, 2011; Lake and Ostling, 2009; Messier *et al.*, 2010), individuals the level at which competitive and environmental interactions actually occur (Clark, 2010; Jung *et al.*, 2010; Siefert, 2012; Violle *et al.*, 2012). To this end, studies which have incorporated intra-specific variability have found an increased ability to detect niche and filtering processes (e.g., Cornwell and Ackerly, 2009; Jung

et al., 2010; Lepš *et al.*, 2011; Siefert, 2012) though the level at which such variation is incorporated within community ecology is still largely restricted to the use of site-specific (i.e., population) means (but see Paine *et al.*, 2011). With respect to this body of literature, it must be noted that community structure is determined based on snap-shot observational data, the process of community assembly not actually followed and thus the structure found and mechanism assigned potentially only transient if the sampled community was not at a stable equilibrium (Drake, 1991; Helsen *et al.*, 2012; Samuels and Drake, 1997).

In contrast it is exactly the process of community assembly which is the basis of studies within the second group, investigating whether assembly follows deterministic or stochastic trajectories, structured by niche-based processes or influenced by historical contingency (i.e., priority effects), respectively (Gray, 2012; Helsen *et al.*, 2012; Matthews and Marsh-Matthews, 2006). To do so, studies have generally either followed the natural re-colonization (re-assembly) of experimentally (e.g., Lonzarich *et al.*, 1998; Meffe and Sheldon, 1990; Sheldon and Meffe, 1995; Simberloff and Wilson, 1970) or naturally (i.e., drought, flood; Bayley and Osborne, 1993; Grossman *et al.*, 1998; Matthews *et al.*, 2013) defaunated areas to determine if community structure returns to the pre-disturbance state, or have artificially constructed communities within similar abiotic conditions with the same initial composition (e.g., Matthews and Marsh-Matthews, 2006) but different orders of species entry (e.g., Chase, 2010; Drake, 1991; Jiang *et al.*, 2011) to determine if similar community structures would develop. Within such studies, much as with trait-based assembly above, more deterministic (filtered) assembly, similar communities across similar environments, have been found within harsher environments (i.e., low productivity, high disturbance) (Chase, 2003, 2010; Fukami and Lee, 2006). Here it must be noted that studies within this body of literature still largely focus on temporal compositional changes, calculating metrics such as Jaccard or Bray-Curtis

dissimilarity indices, comparing species richness's and abundances (Chase, 2010; Gray, 2012; Jenkins and Buikema, 1998; Matthews and Marsh-Matthews, 2006), and that while communities may vary compositionally, both between communities and with the environment, different structural patterns may be found with respect to traits. Indeed this was the case within Fukami *et al.* (2005) who manipulated the order of species entry within environmentally similar cleared grasslands, finding compositional divergence but trait convergence between communities over time; here within-community trait patterns not considered.

Within the present study, our goal was to bridge the gap between these two groups of literature, to follow the trajectory of trait-based community assembly and investigate how both overall and within-community trait relationships vary temporally and as a function of environmental selectivity. The use of streams and stream-fish provide an ideal system in which to do so, streams spatially heterogeneous comprised of discrete riffle, run and pool habitat sections which differ in depth, water velocity and substrate composition (Brown and Brussock, 1991; Lamouroux and Cattanéo, 2006; Rodríguez, 1995), placing different selective pressures on the species and phenotypes able to be found within (Lamouroux *et al.*, 2002; Poff and Allan, 1995; Pyron and Lauer, 2004). Here we performed a defaunation experiment within a stream reach comprising multiple habitat types and sections (i.e., sites, communities) and followed natural fish re-colonization (community assembly) over several re-sampling periods, where it was expected that species and individuals found in different habitat types would differ in their morphology and that the morphologies present within communities would become more similar to pre-defaunation (pre-disturbance) states through time. As riffles are perhaps more selective, placing larger energetic demands on and requiring a greater swimming capacity of the individuals within (Lonzarich *et al.*, 1998; Rodríguez, 1995), as well as being more influenced by temporal fluctuations in water flow (Aaland, 1993; Brown and Brussock, 1991), an extremely

structuring variable within streams (Grossman and Sabo, 2010; Hoeinghaus *et al.*, 2007; Poff and Allan, 1995), we expected the trait space occupied and the average nearest neighbour distance between individuals to be smaller, indicating a greater role of habitat filtering over competition, and that these metrics would follow a more deterministic trajectory toward pre-disturbance states, compared to communities located in more benign pool environments. As we were also interested in incorporating intra-specific trait variation, analyses were conducted using all individuals within the entire stream community, as well as, individually, the two most abundant species found, benthic longnose dace, most associated with riffles, and mid-water column creek chub, most associated with pools (Bernatchez and Giroux, 2000). Findings from this study and comparisons between community and component species temporal patterns provide a more detailed understanding of community structure and represent a potential next step in analyses of the process of community assembly.

3.3 Materials and methods

3.3.1 Stream measurements and site characterization

A stream containing multiple repeating riffle, run and pool habitat sections located close to the Université de Montréal Station de biologie des Laurentides in Saint-Hippolyte, QC, Canada was selected for the complete removal (defaunation) experiment. Within, a roughly 400m reach was sectioned off and environmental characteristics were measured along transects spaced 10m apart (Meffe and Sheldon, 1990) at which bank GPS coordinates, wetted width and percentage substrate composition (boulder, rock, pebble, gravel, sand, wood, mud or macrophyte) were recorded, along with, at the center, stream depth and water flow (at ½ depth; Peres-Neto, 2004) (flow measuring probe; Höntzsch Instruments) (Grossman *et al.*, 1998;

Hoeinghaus *et al.*, 2007). Habitat sections (i.e., sites) within the reach were defined based on characteristically differentiated water flow, depth and substrate composition which can be easily visually identified; transects within each site were averaged to give a single value (Table 3.1).

A total of 14 habitat sections, 3 riffle, 6 run and 5 pool, were identified within the stream (Figure 3.1A). Habitat sections characterized as riffles (average width: 3.96m, depth: 20.04cm, flow: 0.42m/s) were composed primarily of boulder, rock and pebble substrates, runs (average width 4.67m, depth: 17.44cm, flow: 0.35m/s) with rock, pebble and sand substrate composition and pools (average width 4.97m, depth: 46.8cm, flow: 0.24m/s) sand, mud and boulder substrates; habitat types were significantly different according to univariate analyses of variance (ANOVAs) based on all transects for water flow ($F(2,38)=9.851$, $p=0.0004$) and depth ($F(2,38)=12.280$, $p=0.0008$)) but did not differ significantly in terms of width ($F(2,38)=2.802$, $p=0.0733$). Individuals found within a site (i.e., riffle, run or pool) were considered part of the same community (Matthews and Marsh-Matthews, 2006; Meffe and Sheldon, 1990).

Table 3.1. Average environmental characteristics of the habitat sections (sites) delineated within the defaunated stream reach. Transects are the number conducted within the site, averaged for the values presented. For substrate composition: B is boulder, R rock, P pebble, G gravel, S sand, W wood and Macro macrophytes.

Section	Type	Transects	Length (m)	Width (m)	Depth (cm)	Flow (m/s)	Substrate (%)							
							B	R	P	G	S	Mud	W	Macro
1	Riffle	3	30.6	3.3	26.67	0.43	0	45	33.33	13.33	6.67	0	0	1.67
2	Riffle	4	37.1	3.28	18.95	0.53	48.75	36.25	6.25	4.25	2	0	0	0
3	Run	2	23.5	5.6	15.25	0.46	5	25	40	15	15	0	0	0
4	Run	4	39.5	4.65	14.38	0.33	11.25	30	31.25	10	17.5	0	0	0
5	Riffle	3	28.7	5.3	14.5	0.31	52.33	31.67	8.33	2.67	5	0	3.33	0
6	Run	2	19	5	20.25	0.27	20	37.5	37.5	0	2.5	0	2.5	0
7	Pool	2	16.7	5.6	13.5	0.16	25	7.5	12.5	27.5	22.5	0	5	0
8	Run	4	35.3	4.28	13.25	0.39	0	39.88	43.63	8.75	5	0	2.75	0
9	Run	4	42	4.5	17.5	0.3	13.75	40	20	4.25	13.75	0	5.75	0
10	Pool	2	22.7	4.1	20.35	0.32	37.5	35	9	7.5	11	0	0	0
11	Run	3	33.1	3.97	24	0.33	6.67	26	16.67	10	26	0	14.33	0
12	Pool	3	30.6	4.5	47.33	0.26	8.33	15	10	16.67	44	0	2.67	0
13	Pool	3	30.6	5.43	86.07	0.23	13.33	5	0	12.33	60	0	8.33	1
14	Pool	2	23.5	5.2	66.75	0.23	22.5	0	0	0	5	65	2.5	5

3.3.2 Stream clearing and re-assembly sampling

Initial stream defaunation took place over July 1 and 2, 2010, where, due to time constraints, sections 1-7 were cleared on day 1 and 8-14 on day 2, during which time block nets were temporarily installed at downstream, upstream and mid-stream locations. On each day individuals were collected by conducting 3-pass zigzag backpack electrofishing (HallTech Aquatic Research Inc.) proceeding upstream (Smith and Kraft, 2005), individuals collected from each section held in separate floating nets in order to be able to later characterize initial (i.e., pre-defaunation/disturbance) community structure. After collection, individuals were anesthetized using a 1 clove oil: 10 ethanol mixture (active agent eugenol) (Keene *et al.*, 1998; Munday and Wilson, 1997), given a unique subcutaneous VIE tag (visible implant elastomer; Northwest Marine Technologies) using a combination of several fluorescent colours and body locations, photographed on one lateral side in order to later consider morphology and measured for standard length. After processing, individuals were divided into two even re-introduction groups and were released back

into the stream, downstream within section 3 and upstream within section 12 (Figure 3.1A). Note that individuals found on day 2 (within sections 8-14) which had been processed and released on day 1 were returned back into the section in which they were found, their re-capture not included within the "initial community composition" of that section.

In order to follow the re-assembly of communities within cleared habitat sections, the entire reach was backpack electrofished every 5 days for 4 samplings, sample 1 (S1) which took place on July 7, sample 2 (S2) on July 12 and sample 3 (S3) on July 17 were conducted using upstream single-pass zigzag backpack electrofishing, the final sample (S4) was conducted over two days, July 22 and 23, as per initial clearing. Although the goal was to attain a detailed investigation of temporal community re-assembly and it is known that stream-fish re-colonize rapidly after defaunation (Sheldon and Meffe, 1995), sampling was conducted every 5 days as previous experience informed that sampling more frequently caused fish avoidance of the electrofished area (B. Jacobson, *personal observation*). For the duration of each sampling day, a block net was installed at the upstream end of the reach where, after collection within a habitat section was complete, each individual was investigated for a VIE tag and if none was found the individual was anesthetized, photographed, measured and then released back within the site.

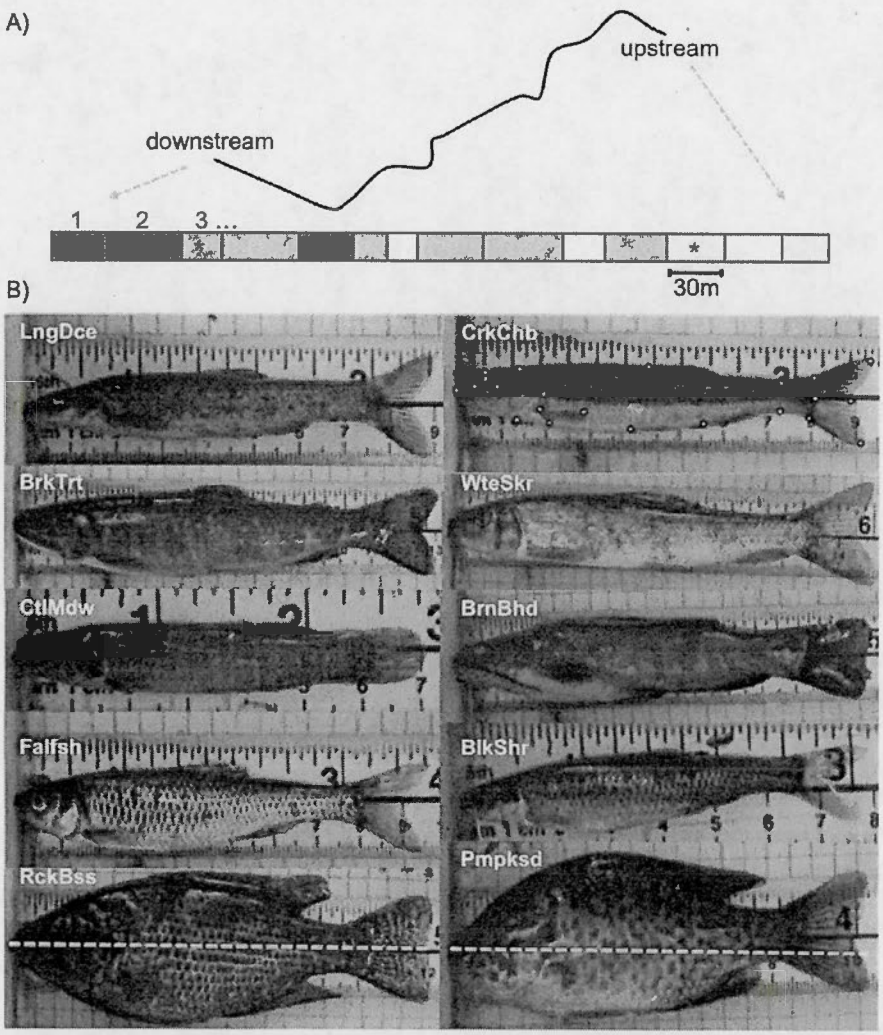

Figure 3.1. The defaunated stream reach and the species found within. A) Stream reach where orientation and drawing is based on GPS coordinates of transects, and dark grey boxes are riffle, light grey run and white pool habitat sections; stars denote areas of release. B) All species collected across samplings, see text for common names represented by species codes. The two bottom species were removed from morphological analyses, morphometric landmarks within CrkChb were the same for all species.

3.3.3 Data analysis

A total of 10 species were found across samplings (Figure 3.1B; Table 3.2): longnose dace (*Rhinichthys cataractae*; LngDce), creek chub (*Semotilus atromaculatus*; CrkChb), brook trout (*Salvelinus fontinalis*; BrkTrt), white sucker (*Catostomus commersoni*; WteSkr), central mudminnow (*Umbra limi*; CtlMdw), brown bullhead (*Ictalurus nebulosus*; BrnBhd), fallfish (*Semotilus corporalis*; Falfsh), blackchin shiner (*Notropis heterdon*; BlkShr), rock bass (*Ambloplites rupestris*; RckBss) and pumpkinseed (*Lepomis gibbosus*; Pmpksd) (Bernatchez and Giroux, 2000). Due to drastically differing morphologies rock bass (n=28) and pumpkinseed (n=1) were not included within analyses; also, due to problems with positioning for pictures (pectoral spines pointing perpendicularly), 5 incidences of brown bullhead are not included, these exclusions are shown within Table 3.2.

For all remaining species and individuals, 22 homologous landmarks were digitized on photographs (Figure 3.1B) using the program tpsDIG2 (Rohlf, 2005a), geometric morphometrics used for trait considerations. As all analyses were conducted considering 1) the entire stream community (n=1474) and individually 2) longnose dace (n=901) and 3) creek chub (n=347), landmarks were then converted into 3 separate sets of partial warps using the programs Coordgen6 and PCAgen6 (Sheets, 2004a, 2004b).

Table 3.2. Species incidences as a function of the habitat section and sample in which they were found. See text for common names represented by species codes. Initial is the pre-defaunation community, S1- S4 re-assembly sampling 1-4 respectively.

		Species Incidences							
Section	Sample	LngDce	CrkChb	BrkTrt	WteSkr	CtlMdw	BrnBhd	Falfsh	BlkShr
1	Initial	16		6					
Riffle	S1	8	2						
	S2	23	1						
	S3	12	1						
	S4	20				1			
2	Initial	34	14	7					
Riffle	S1	18	2						
	S2	13							
	S3	22	2						
	S4	40	2						
3	Initial	15	12						
Run	S1	13	7			1			
	S2	13	7			1			
	S3	18				1			
	S4	18				1			
4	Initial	16	13	5					
Run	S1	19	18			2		1	
	S2	19	5						
	S3	21	6			1			
	S4	26	3						
5	Initial	35	2	12					
Riffle	S1	13	2			1			
	S2	17	9						
	S3	16	6						
	S4	18	2	1					
6	Initial	16	11	6					
Run	S1	14	8			1			
	S2	9	8			1			
	S3	15	7						
	S4	31	12						
7	Initial	2	7			3		2	
Pool	S1	2	3					1	
	S2	7	8			2			1
	S3	3							
	S4	8	3						
8	Initial	33	12	8				1	
Run	S1	23	1						
	S2	16	5						
	S3	24	2			1			
	S4	26	1						
9	Initial	44	12	11		3		3	
Run	S1	23	4						
	S2	27	4			1			
	S3	20	5			2		2	
	S4	27	9	1					
10	Initial	3	19		2	5		1	
Pool	S1	4	10			1			1
	S2	4	7						
	S3	3	9			2		1	
	S4	2	20					2	1
11	Initial	12	3			5			
Run	S1	4	4			2			1
	S2	5	8			4			
	S3	4	3			1			
	S4	4				5		1	
12	Initial	1	4			11			
Pool	S1		1			1			
	S2		3			2			
	S3		1			4			
	S4	2	3			2			
13	Initial		3	1	8		3		1
Pool	S1				1				
	S2		1		18		2		
	S3				1				
	S4			1	1	5	2		
14	Initial		1		1		2		
Pool	S1		1		10			2	
	S2		2	1	2				
	S3		4		7				
	S4		2		5	2	3	1	

3.3.3.1 Overall morphological trends

In order to determine the degree to which phenotypes differed between habitat types, and as such, the overall degree of environmental filtering, a discriminant function analysis (DFA) was performed using partial warps with individuals coded based on within which habitat type (riffle, run or pool) they were found. Deformation grids were produced in order to visualize any morphological differences across individuals using the primary axis of variation (DF1) as the independent variable within the program tpsRegr (Rohlf, 2005b). A DFA with partial warps was also used to follow the trajectory of morphological assembly and view whether patterns of differentiation between samplings appeared deterministic or stochastic, individuals coded based on the sampling period in which they were collected. As within Lonzarich *et al.* (1998) the order of arrival during re-colonization was found to be a function of fish length, univariate ANOVAs were run using $\log_{10}$ transformed standard lengths and sampling period in order to test for the presence of this influence.

3.3.3.2 Within community trait patterns

In order to further investigate community trait structure, two metrics were calculated for each habitat section at each sampling: 1) average distance, which measures the trait volume occupied by the community and degree of habitat filtering, here calculated as the average pair-wise Euclidean distance between all individuals within the community; and 2) average nearest neighbour distance (NND), which estimates the density of niche packing within the community and degree of potential competition, here calculated as the average Euclidean NND between individuals within a species, where for analyses at the stream community level these values were averaged across all species, those with only one individual excluded (Weiher, 2011; Weiher *et al.*, 1998; Winemiller, 1991).

In order to determine if the observed metric value (Obs) for a habitat section was different from what would be expected by chance, observed values were contrasted to a null distribution built on the basis of 999 permutations (observed value being the 1000th value), composing null communities with the same as observed species richness and if possible number of individuals per species by selecting from the entire species pool (all habitats, all samplings); for each permutation, metrics were re-calculated for the null community (null). Here, random selection took place over the entire species pool as all individuals were considered to have access to all communities within the sampled reach (Meffe and Sheldon, 1990) and this allowed for the potential to detect NND differences between habitat types. In order to be able to compare communities, standardized effect sizes (Std) (Jung *et al.*, 2010; Siefert, 2012) were calculated for each metric and habitat section as:

$$\text{Std} = \frac{(\text{Obs} - \text{avg null})}{\sigma \text{null}}$$

where a negative standardized value indicates that the observed metric was smaller than expected by chance, a smaller trait volume occupied or more densely packed niche (i.e., less potential competition) with regards to average distance and average NND, respectively. As we were interested in both how these metrics changed through the re-assembly of communities (i.e., across samplings) and as a function of habitat type, standardized values for each metric were entered as the dependent variable within separate two-way ANOVAs testing the influence of time, habitat type and the time x habitat type interaction. All DFAs and ANOVAs were computed using Statistica 6.0 (StatSoft) and metrics and null models were calculated using MATLAB R2012a (MathWorks).

3.4 Results

Note that while S4 differed from S1-S3 in terms of sampling methodology neither the total abundance ($F(1,54)=3.58$, $p=0.06$) nor species richness ($F(1,54)=1.92$, $p=0.17$) levels found between such samplings differed significantly according to univariate ANOVAs, only 5 of the 14 sections had S4 total abundance higher than S1-S3 (average: 11 range: 2-20). Also, while the length of habitat sections differed, neither total abundance nor species richness was significantly correlated with site length for any of the habitat types (Riffle: $r=0.24$, $p=0.39$; $r=0.24$, $p=0.39$; Run: $r=0.28$, $p=0.13$; $r=0.08$, $p=0.69$; Pool: $r=0.24$, $p=0.24$; $r=0.22$, $p=0.28$, abundance and species richness, respectively). Thus these factors were not considered to have any influence over the findings below.

3.4.1 Overall morphological trends

For the stream community as a whole as well as for each the longnose dace and creek chub separately, individuals within different habitat types were significantly morphologically differentiated according to DFAs (Figure 3.2; Table 3.3), Wilks' lambda values indicating the stream community to be the most, and longnose dace the least, differentiated. For all three DFAs, DF1 primarily differentiated individuals found within riffle and run versus pool habitats, morphologies within riffles and pools always the most dissimilar as evidenced by Mahalanobis distances. As per visualizations from deformation grids, individuals within the riffles and runs were those with more streamlined bodies and forked caudal fins for the stream community, with more streamlined bodies and longer pectoral fins for the longnose dace, and lastly, with more ventrally angled pectoral and larger caudal fins for creek chub (Figure 3.2).

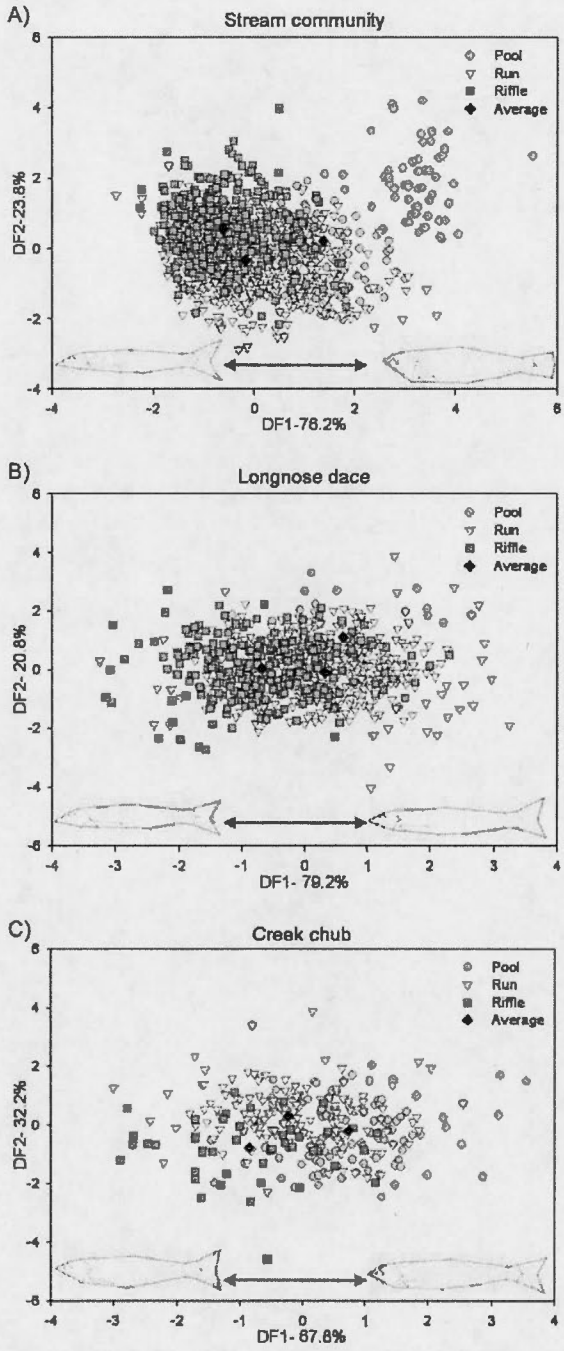

Figure 3.2. Morphological differentiation between habitat types as per DFAs. Deformation grids show relative differences as a function of DF1 where visualization for all is the observed range.

With respect to the morphological trajectory of samplings through time, again for each the stream community, longnose dace and creek chub, DFAs were significant, the morphologies of individuals found within samplings following a path from S1 to S4 towards (i.e., becoming more similar to) the initial pre-defaunation (pre-disturbance) community (Figure 3.3; Table 3.3). Here, with the exception of creek chub which remained the most differentiated in sampling morphologies overall, the Mahalanobis distances between S1-initial community versus S4-initial community were always larger (Table 3.3). As the length of fish found within the stream decreased significantly through time according to univariate ANOVAs for only the stream community ($F(4,1469)=3.24$, $p=0.012$), not significant at the species level (longnose dace: $F(4, 896)=1.954$, $p=0.100$; creek chub: $F(4, 342)=1.226$, $p=0.300$), morphology, not fish length, was considered to play the primary role in dictating re-colonization order.

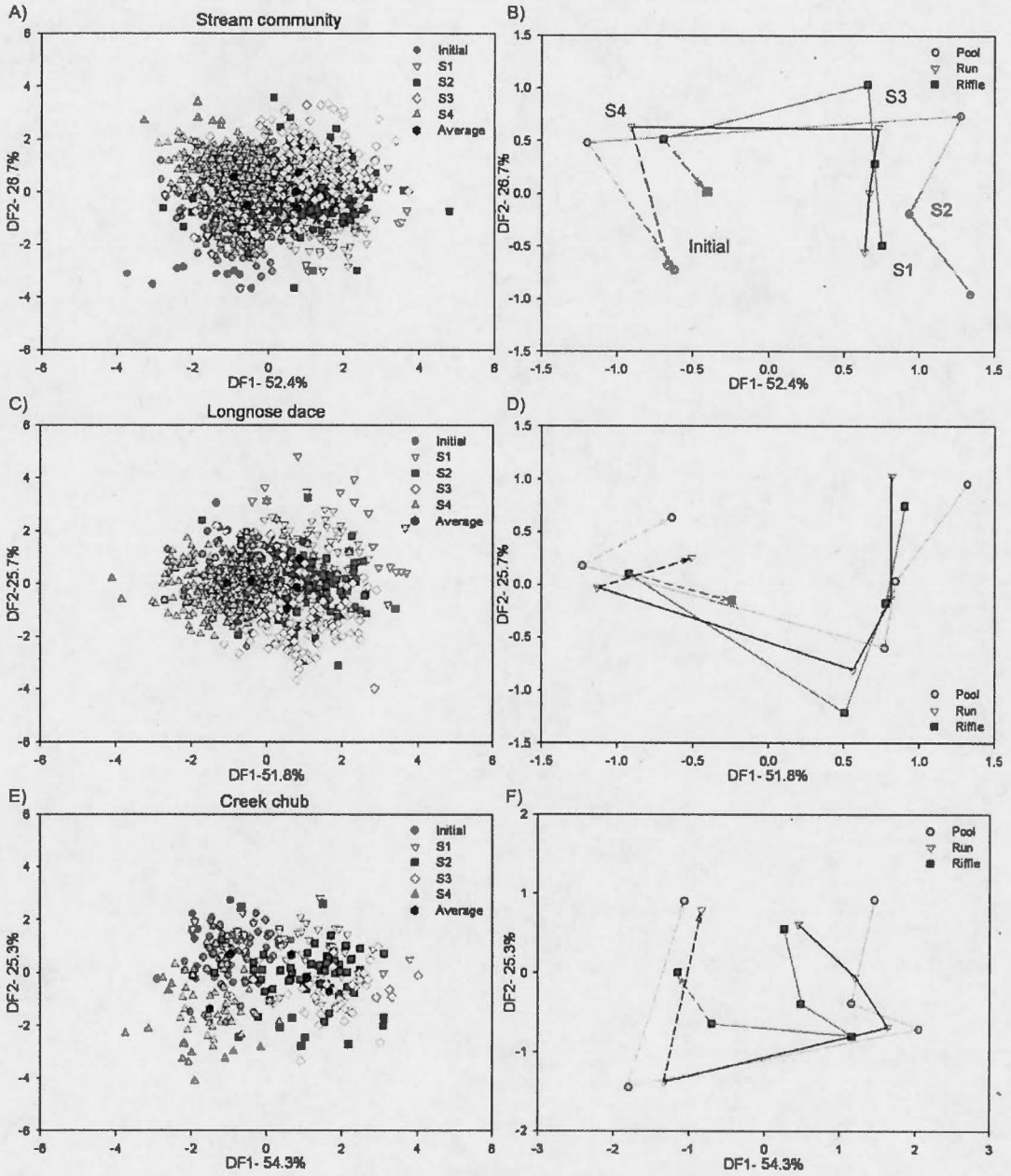

Figure 3.3. Overall morphological changes through sampling period as per DFAs. Panels A, C and E show all data points (individuals) within the analysis, panels B, D and F show the average score for each sampling as a function of habitat type to better visualize trajectory for the stream community (A and B), longnose dace (C and D) and creek chub (E and F).

Table 3.3. Habitat differentiation and morphological trajectory outcomes of discriminant function analyses. All values are significant at $p \leq 0.05$ expect those in italics.

Morphological Analysis	Wilks' lambda	F-value	Mahalanobis distance Pool - Run	Pool - Riffle	Run - Riffle
Habitat differentiation					
Stream community	0.590	10.818	2.724	4.126	0.985
Longnose dace	0.758	3.195	*1.559*	2.827	1.042
Creek chub	0.672	1.678	1.202	2.892	*1.574*
Sampling trajectory			**S1 - Initial**	**S4 - Initial**	
Stream community	0.400	9.214	2.796	1.840	
Longnose dace	0.376	5.942	3.158	1.500	
Creek chub	0.163	4.364	4.592	5.333	

3.4.2 Within community trait patterns

Different patterns in and levels of significance of standardized average distance and average NND metrics were found across time and as a function of habitat type in relation to the stream community versus individual species as per two-way ANOVAs (Figure 3.4; Table 3.4). For the stream community there was no significant difference in the average distance between individuals within the community as a function of either time, habitat or their interaction (although habitat was marginally significant at $p=0.07$), all standardized values for this metric negative; for average NND, however, both time and habitat were significant (Table 3.4) and communities within pools had positive standardized values (i.e., greater NND than expected by chance) for S2 and S3. Here, for both metrics, communities within run and riffle habitat types appeared to have more similar patterns in metric change through time than those in pools, following a more deterministic path towards initial community structure (Figure 3.4). With respect to both longnose dace and creek chub on the other hand, for both metrics, the only factor which was significant according to two-way ANOVAs was time, communities found within different habitats following very similar metric

trajectories which followed, overall, deterministic paths from positive to negative standardized values towards initial community structure (Figure 3.4; Table 3.4).

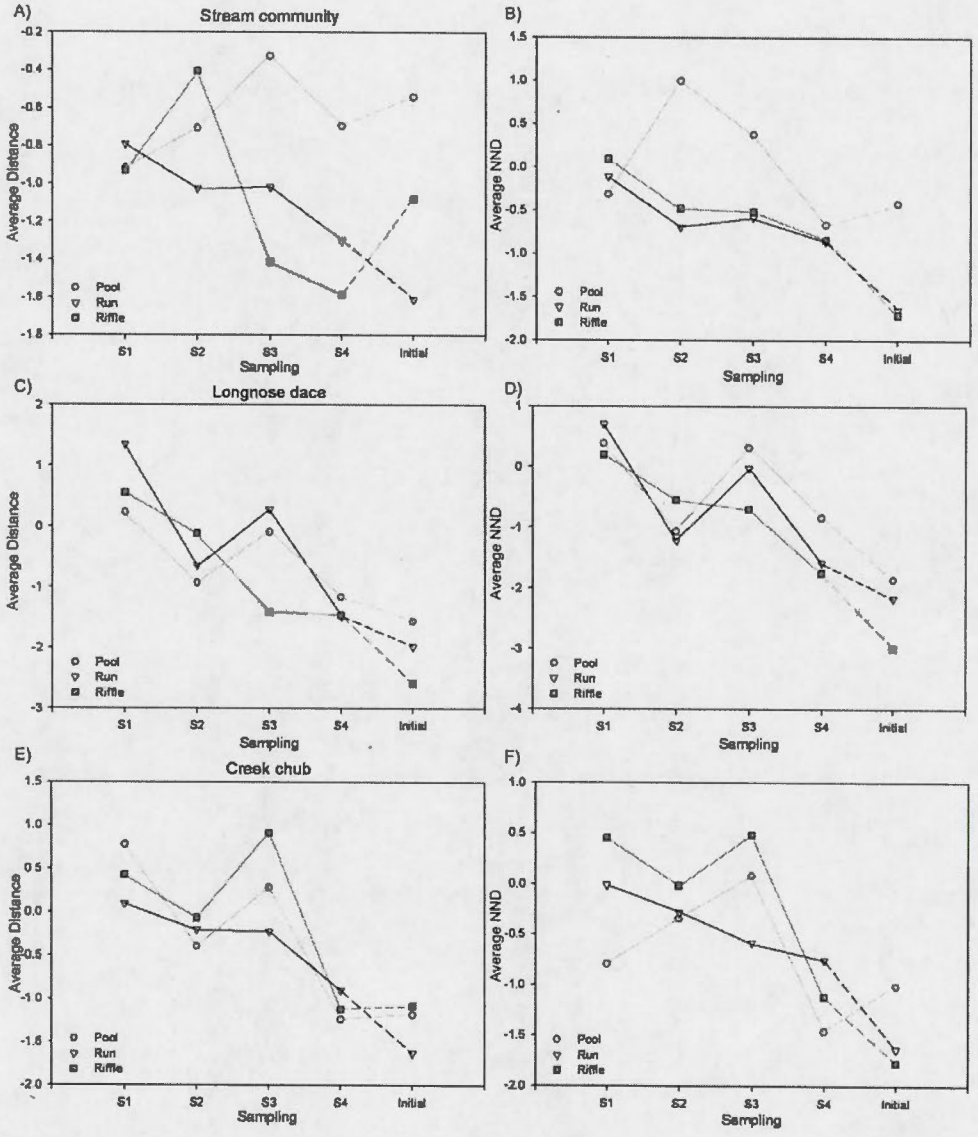

Figure 3.4. Results from two-way ANOVAs of assembly metrics as a function of time and habitat type. Metrics average distance (panels A, C and E) and average NND (nearest neighbour distance; panels B, D and F) are shown for the stream community (A and B), longnose dace (B and C) and creek chub (E and F).

Table 3.4. F-values from two-way ANOVAs regarding the influence of time, habitat and the time x habitat interaction on assembly metrics. Numbers in brackets are the degrees of freedom. Avg dist. is the metric average distance, NND the average nearest neighbour distance.

Factor	Stream community		Longnose dace		Creek chub	
	Avg dist.	NND	Avg dist.	NND	Avg dist.	NND
Time (4)	0.671	6.347**	9.567**	9.895**	3.233*	2.971*
Habitat (2)	2.793	7.550*	1.246	0.927	0.536	0.224
TxH (8)	0.787	1.589	0.978	0.483	0.311	0.488

p≤0.05*
p≤0.001**

3.5 Discussion

3.5.1 Re-assembly of the stream community

As expected, individuals found within different habitat types were significantly differentiated in their morphologies, morphological values returning through sampling towards pre-disturbance (pre-defaunation) states, morphologies within the final sampling most similar to initial values. These findings strongly suggest the action of niche-based processes in sorting phenotypes across the system and through time, environmental filtering at the level of the stream reach occurring as phenotypes within each habitat type were a subset of the total morphological variation within the system, this mechanism proposed to shift trait means and restrict ranges (Jung *et al.*, 2010; Kraft *et al.*, 2008). Such phenotypic sorting was considered to be a function of differential swimming ability, water velocity the main structuring variable across habitat types (Lamouroux *et al.*, 2002; Pyron and Lauer, 2004), where as per deformation grids individuals within riffle and run habitat sections were those best adapted for their use, a more streamlined body shape and forked caudal fin linked

with swimming capacity within energetically demanding environments (Gatz, 1979; Leavy and Bonner, 2009).

With respect to within community trait patterns, standardized average distance and average NND were found to show different patterns through time as a function of habitat type, as per two-way ANOVAs. Here, as expected, communities within riffles and runs were more deterministic than those within pools, the negative standardized values of both average distance and average NND metrics decreasing through time towards pre-disturbance community structure. Such metric values, as has been proposed within streams (Grossman and Sabo, 2010; Hoeinghaus *et al.*, 2007; Jackson *et al.*, 2001), indicate a greater role of habitat versus biotic filtering (i.e., competition), the trait space occupied and NND less than expected by chance, dense niche packing related to less of a limit to similarity; deterministic assembly and trait under-dispersion proposed to be associated with and found exactly in harsher environmental conditions (Chase, 2003, 2010; Fukami and Lee, 2006). Note that while we may have expected pool communities to have overall positive standardized metric values (i.e., unfiltered trait space and larger NND), being more benign and less restrictive, the negative standardized values found (which were still less so than those of riffles and runs) were perhaps a necessary outcome given that the null distribution sampled across, and morphologies were found to be differentiated between (as per DFA), all habitat types.

3.5.2 Species-level structure and intra-specific variation

With respect to individual-level analyses of both longnose dace and creek chub, as at the stream community level, individuals were found to be morphologically differentiated between habitat types with communities (populations) showing

deterministic trajectories of assembly towards pre-disturbance morphological values, indicating again habitat filtering and phenotypic sorting (Jung *et al.*, 2010; Kraft *et al.*, 2008), here at the individual species level. Differences were found, however, between these two species, where, as per DFAs, communities of longnose dace remained less differentiated between habitat types, and returned to pre-disturbance values more so, than those of creek chub. This was accounted for through the differential ability of these species to use the environments found throughout the stream reach. Indeed, longnose dace, a benthic species most associated with fast flowing areas (Bernatchez and Giroux, 2000), is known to be less influenced by the energetic demands of habitats, buffered by substrate, the longer pectoral fins of individuals found within riffles (as per deformation grids) allowing for an increased ability to hold station against current (Gatz, 1979), this species, unlike some other benthics, also having the capacity to hold station by swimming in particularly high flow conditions (Facey and Grossman, 1992). Creek chub on the other hand, a mid-water column species most associated with low flow areas (Bernatchez and Giroux, 2000), may be greatly influenced by swimming demands, as while the lower angled pectoral fins of individuals found within riffles and runs (as per deformation grids) allow for decreased energy expenditure (Eidietis *et al.*, 2002), movement of this species has been found to be impeded by patch velocities as well as lengths (Belica and Rahel, 2008; Lonzarich *et al.*, 2000). Thus the greater return to pre-disturbance states of longnose dace may be explained by sampling ability, the greater differentiation between habitat types of creek chub explained by a greater exclusion from particular areas (i.e., high flow) due to swimming capacity.

In contrast to the overall morphological trends, and what was found at the stream community level, here both species as well as both metrics showed similar patterns through time, between habitat types, time the only significant factor as per two-way ANOVAs. Indeed in mostly all cases, metrics started (i.e., S1) with positive

standardized values decreasing, in an almost step-wise fashion, towards pre-disturbance community structures, indicating a potential combined role of habitat filtering and competition; communities re-ordering through time by adding and subtracting morphologies to/from the periphery of community trait space, this re-ordering shifting the average morphological space through time, as per DFAs showing assembly trajectory.

3.5.3 Synthesis and next steps for trait-based community assembly

The goal of our study was to bridge the gap between the two complementary groups of community assembly studies that can be found in the current literature, to use a temporal trait-based approach to investigate the process of assembly and development of community structure and how this may vary as a function of environmental selectivity. Here, for all analyses, both at the level of overall morphological trajectory and within community trait patterns, considering the entire stream community, or the most abundant species individually, communities were found to vary as a function of sampling period. This illustrates, then, the importance of integrating the two types of studies, pointing to a potential need for caution in conclusions drawn regarding the community structure found and assembly mechanism assigned within studies using only snap-shot trait-data. In addition, that morphologies were differentiated between habitat types and the trajectories in overall trait values and within community structure were found to be largely deterministic, with the exception of stream communities within pools, irrespective of differences in compositional attributes (or similarities at the species level) shows that trait-environment linkages are highly structured, potentially providing a better functional understanding of patterns of landscape distribution than that afforded through taxonomic considerations, again illustrating the need for the integration of the two bodies of assembly literature.

Note that within this study it was particularly interesting that within community trait patterns were found to show different trends and degrees of filtering, both through time and as a function of habitat selectivity, at the stream community versus independent species levels. Thereby, in addition to continuing to integrate temporal considerations in trait-based community assembly, and exploring how patterns may change across heterogeneous landscapes, a potential next step for future studies would be to explore further the degree to which different species within the same community are differentially influenced by abiotic and biotic factors, how the independent structures of component species ultimately add to determine observed community structure.

CHAPTER IV

QUANTIFYING AND DISENTANGLING DISPERSAL IN METACOMMUNITIES: HOW CLOSE HAVE WE COME? HOW FAR IS THERE TO GO?

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4.1 Summary

Much of ecological research centers around discovering the underlying factors for species distribution; three such factors are of central importance: local environment, landscape features and dispersal. While all have been simplified in the past, the recent increase in metapopulation and metacommunity research makes being able to quantify dispersal all that much more necessary. In order to increase our knowledge about metacommunities in the ''real word'', it is clearly time to start thinking critically about whether and how the methods that are currently available for measuring dispersal within metapopulations can be adapted. The goal of this contribution is to present and argue the technical difficulties involved in measuring dispersal within metacommunities through: (1) discussing the merits and pitfalls of some potential direct (e.g., mark-recapture) and indirect methods (e.g., isolation measures, patchiness) for studying the effects of dispersal at the metapopulation and metacommunity level; (2) discuss the types of questions that can be tackled at the metacommunity level in light of methodological decisions; and (3) make the point that the technical difficulties of measuring dispersal for multiple species may leave us with little other options than using indirect methods to estimate dispersal in metacommunities.

4.2 Introduction

Much of ecology is concerned with accounting for patterns of species distribution and understanding the factors which cause these patterns. Dispersal, emigration from and immigration to a particular area (Leibold *et al.*, 2004; Semlitsch, 2008), is a pervasive process which acts to structure the distribution of species (Dieckmann *et al.*, 1999) over multiple temporal and spatial scales (Nathan, 2001). The recent increase of interest in dispersal has, in large part, been due to the development of the metapopulation and metacommunity paradigms; metapopulations - networks, connected through dispersal, of single species populations within internally homogeneous habitat patches embedded in an unsuitable homogeneous matrix (Baguette, 2004; Leibold *et al.*, 2004), and metacommunities differing through the consideration of multiple species and relaxation of environmental homogeneity (Leibold *et al.*, 2004). As such, it would seem intuitive to think that empirical research based on dispersal is well rooted, with proven accurate methods to quantify this process readily available for use in such research.

Although the metapopulation and metacommunity concepts are now somewhat well established ecological paradigms, our ability to measure dispersal directly (e.g., mark-recapture methods) is still lacking, causing empirical work to fall far behind of theoretical developments. This is especially the case within metacommunities where tracking multiple species may prove to be a difficult task. As the effects of system heterogeneity were overlooked in order to simplify models (Wiens *et al.*, 1993) and the patterns and processes found were thought to be constant across all scales (Leibold *et al.*, 2004), it is perhaps not surprising then that the few methods that are available for quantifying dispersal within metacommunities are in many cases highly simplified and abstracted from ecological reality (Travis and French, 2000). In addition to the fact that system heterogeneity and dispersal jointly affect the

distribution of species, their relative strength in doing so also changes across scales even within the same system (Freestone and Inouye, 2006) thereby making these three previously overlooked but important factors intricately interwoven; additionally complicating the techniques needed to accurately quantify and disentangle dispersal.

Although the technical issues involving the estimation of how dispersal structures metapopulations have already generated much discussion, these challenges in regards to metacommunities are still much deserving of a proper appraisal. Given that metacommunity ecology is a relatively new and exciting field, it is reasonable that our understanding of metacommunities in the ''real word'' is lagging behind, especially since much of our knowledge about the influence of dispersal comes from small-scale experiments where dispersal has been manipulated directly and not tracked. Clearly, though, we need to start thinking critically about the challenges involved in estimating the importance of dispersal involving metacommunities. Therefore, our goal here is not to review the roles of dispersal in structuring metacommunities (see Leibold *et al.*, 2004 for a review), but instead to provide a critical review on the issues and technical difficulties/challenges involved in quantifying dispersal within metacommunities. More specifically, we will (1) discuss the merits and pitfalls of some potential direct (e.g., mark-recapture) and indirect methods (e.g., isolation measures, patchiness) for studying the effects of dispersal at the metapopulation and metacommunity level; (2) discuss the types of questions that can be tackled at the metacommunity level in light of methodological decisions; and (3) make the point that the technical difficulties of measuring dispersal for multiple species may leave us with little other option than using indirect methods to estimate dispersal in metacommunities.

Whether the use of indirect quantification techniques is sufficient, of course, depends in part on the questions being asked and how information is being collected and in

some cases within metacommunity research it may be imperative to use direct methods despite the technical difficulties involved. It is only by critically analyzing how techniques for quantifying dispersal are used and their limitations that we will be able to judge how far there is to go in order to be able to accurately quantify the consequences of this phenomenon in structuring ecological communities. Ultimately, decisions regarding which methods are implemented may be made on the basis of the technical difficulties encountered and the consequent simplifications, but we feel that it is important to argue the consequences of these decisions and their inherited limitations. Thereby, we hope that this contribution will provide a resourceful starting point and act as a stepping stone for the advancement of dispersal research, leading to more accurate views of how dispersal is currently captured and motivating ecologists to develop and identify the most appropriate methods to quantify dispersal while answering questions regarding their metacommunity.

4.3 Dispersal: differentiating and locating

Before further discussion involving the quantification of dispersal it is important to have a clear understanding of how dispersal differs from other organism relocation. While theory is developed with a detailed definition of dispersal, this definition often changes for model development, lab experiments and field studies with researchers using a working definition reflecting their ability to measure or model organism relocation. In order to be able to directly compare empirical findings with theory either the same definition must be used or it shown that the mechanism being defined does not have differential consequences to our understanding of metacommunities; that the same overall process is being captured despite different working definitions. We believe that the former (i.e., using consistent definitions of dispersal), is a more sensible idea to follow as we discuss below. Organism relocation can take one of three forms: movement, migration or dispersal. As these three different categories

may have very different consequences for population dynamics and persistence, it is important that researchers use them accordingly.

Movement works on the smallest scale, and occurs when an individual forages for food, searches, and more generally, encompasses any behavior (e.g., sampling) within the organism's home range (McMahon and Matter, 2006). As such, this form of organism relocation may have little or no effect on overall metapopulation or metacommunity system persistence across landscapes as no inter-patch exchange occurs. In contrast migration is defined as round-trip relocation, such that individuals move from one population to another, remain for a relatively extended period of time and then return to the source population (Nathan *et al.*, 2003). Lastly, dispersal involves unidirectional movement from one population to another (Leibold *et al.*, 2004; Nathan, 2001; Semlitsch, 2008) and as such impacts system persistence and affects the dynamics of both the populations from which the individual emigrates and into which it immigrates. It is important to note that dispersal occurrence may relate to the density of the source and target populations such that dispersal may be either positively or negatively density dependant or density independent (Nathan, 2001; Travis and French, 2000). Due to their differences, migration and dispersal are linked to different scales, migration to the population scale and dispersal to the landscape and metapopulation/metacommunity scales (Semlitsch, 2008). Understanding the difference between these three processes is key to understanding their effects on the rest of the system, which scales are being considered and how they should be quantified. Unfortunately migration and dispersal are at times used interchangeably, as is the same with dispersal and movement, dispersal used as a catch-all term for organism relocation.

Dispersal occurs over different distances and in multiple positions in reference to a system, affecting the accuracy with which it can be captured. That variable distances

are traveled during dispersal is evident from frequency distributions of dispersal distances of a population, the dispersal kernel, which generally depict high rates of short distance dispersal (hereafter SDD) and rare cases of long distance dispersal (LDD; Nathan, 2001; Nathan *et al.*, 2003). In order to differentiate and define the threshold between SDD and LDD mechanistic methods have been developed (e.g., incorporating parameters reflecting dispersal traits); however many studies make this distinction based on the attributes and scale of the specific study and organism involved, thereby making the distinction somewhat arbitrarily (e.g., choosing a distance value known to be higher than the average dispersal distance within the system; Nathan *et al.*, 2003). These decisions most likely introduce potential error especially when considering metacommunities where these errors may add across species. Due in part to the difference in frequency and difficulties in measuring LDD, research in this area has only recently started to gain attention, creating two separate bodies of research, that considering dispersal and that specifically regarding LDD. Thereby, while SDD remains the dispersal form of focus within current research, the importance of LDD within these systems is not unacknowledged as it acts over large scales and thus has a large effect on species colonization and gene flow and is linked to invasiveness (Nathan, 2001; Nathan *et al.*, 2003). However, despite the noted importance of LDD events for metacommunities, LDD may be less important than SDD considering the number of species present within these systems. Indeed the tradeoff between the sampling range and therefore labor needed to quantify LDD within a metacommunity and the small gain of information for a relatively small fraction of the individuals hazards against the consideration of LDD within these systems. That being said, ecologists need to explore the short and long term consequences of SDD versus LDD in metapopulation and metacommunity dynamics in order to determine if LDD quantification is necessary to answer the questions posed. LDD will not be explicitly considered and therefore specifics will not be presented, for a detailed discussion on the concept and methods of quantification see Nathan *et al.* (2003) and Nathan (2005). Again, our goal is not to review if and how

dispersal affects metacommunities. However, some of this discussion is necessary for the sake of exploring how much understanding can be gained or lost by tackling or not the technical difficulties involved in measuring dispersal.

Although the focus within metapopulation and metacommunity systems is dispersal between patches (within system), dispersal also occurs in other locations relative to the system; for example external emigration which provides individuals and propagules from outside of the metacommunity. In fact, dispersal occurring within and between metacommunities or between a metacommunity and an outside species pool has been found to differently affect species richness at local and metacommunity scales (Cadotte and Fukami, 2005; Fukami, 2005). Within metapopulations differing locations of dispersal, either from external sources or internally, may affect population dynamics where dispersal may colonize an unoccupied patch or change local density, external dispersal altering the number of individuals within the system. Therefore it is clear that, theoretically, studies investigating metapopulation and metacommunity systems should also consider the effects of dispersal from all locations.

4.4 Measuring dispersal: direct versus indirect methods

Whether certain measures are considered direct or indirect may depend on how researchers have chosen to make this distinction. Here direct methods focus on the dispersing organism itself, measuring this process through marking and organism re-location thereby only considering current dispersal while indirect methods refer to those which are based or partially based on the spatial structure of the study system. Indirect methods assume first that dispersal occurs and second that the ecological model applied is able to capture the signatures of previous dispersal and/or

potential/future dispersal. Therefore, indirect methods are based on measures of habitat connectivity that serve as proxies of dispersal. Schumaker (1996 and references therein) made the point that useful indexes of connectivity should correlate strongly with dispersal processes, though in many instances they may more accurately describe potential rather than realized dispersal. Under this view, in fact, indirect methods can potentially measure the combined effects of past and future dispersal and can perhaps provide better insight especially when there is temporal variation in dispersal (see temporal heterogeneity discussion below); direct methods may only be able to capture part of the overall dispersal dynamics, especially if dispersal behavior encompasses greater temporal scales than the sampling duration in which dispersal was quantified. This may be particularly important in the case of metacommunities, which may be composed of many different species that disperse at many different temporal scales.

For both metapopulation and metacommunity research, which type of method, direct or indirect, should be employed will depend on the questions being asked. Should researchers be interested in individual properties (e.g., traits, behavior) and/or system structure (e.g., actual corridors used for dispersing, whether individuals did not establish in local sites due to corridor quality while dispersing or local patch quality at arrival) then direct methods must be used; however, if less detailed information about individuals is necessary than indirect methods are perhaps sufficient. When assessing the importance of dispersal at least six questions come to mind: (1) how many individuals left from and/or arrived at a particular site?; (2) which individuals arrived to and left a particular site (i.e., individual tracking)?; (3) which sites did the dispersers come from?; (4) what were the paths used while dispersing?; (5) which are the optimal and non-optimal paths in the landscape for dispersal? and (6) do dispersal patterns change through time? Direct methods would have to be used in order to assess questions 1-4, whereas indirect methods could be used to assess question 5 and

depending on certain assumptions (i.e., number of individuals arriving are greater than being born and number of individuals leaving are greater than mortality) question 1. Lastly, question 6 may be answered theoretically through a combination of time series and indirect methods, and empirically through the long term application of direct methods. Therefore depending on which of the questions above are of interest to the researcher regarding dispersal within their studied systems, different methods may be utilized to best determine the answer.

4.5 Measuring dispersal: the metapopulation view

At first glance, it would be logical to assume that measuring dispersal at the metacommunity level would be a simple matter of applying the quantification methods of metapopulations to metacommunities. Although this may be permissible for certain metacommunities (dependant on the taxa), a multi-metapopulation view will not be feasible nor desirable for all, and a combination of methods may have to be used. The major challenge for metacommunities is the presence of different species with different dispersal behaviors, capability and scales. Through determining the technical limitations involved with the methods used for single metapopulations it may be possible to see if adapting these for metacommunity use would be a worthwhile starting point for the advancement of dispersal quantification within metacommunities.

4.5.1 Direct methods

Here we provide a small account of the direct methods used in metapopulation research as a way to understand the type of information gathered and the questions that can be answered, which in turn will aid in determining how they can be used in

the metacommunity context, where such methods do not currently exist. This is by no means an exhaustive list. While a quantification method may be classified overall as direct there can be considered a hierarchy of specificity within this category which depends on how individuals are tracked and the degree of detail about the dispersal event that is elucidated. Perhaps the most general of the available direct methods is stable isotope enrichment, a form of mark-recapture study which marks populations passively through incorporation of the isotope (mark) into the individual through, for example, resource consumption. While stable isotopes occur naturally at differing concentrations within the environment large expanses of geography will often have the same natural isotopic concentration and therefore will only be useful for quantifying LDD (Hobson, 2005). Enrichment is thereby used to circumvent this issue through increasing the concentration within a specific area above natural/surrounding levels. It must be noted that even with enrichment, limitations exist regarding this technique as it is best used to quantify the dispersal of small organisms which occur in discrete populations, which allows marking to take place more readily from isotope integration into the food web (Hobson, 2005). In addition the number of patches within the metapopulation that can be tracked is often limited as in many cases studies use only a single isotope (Hobson, 2005), however the use of multiple isotopes eliminates this problem (Caudill, 2003; Hobson, 2005).

More direct (classic) mark-recapture procedures, where individuals are marked separately, also overcome the patch number limitation as individual marking allows researchers to determine immigration and emigration to and from many patches within a system. In addition, unlike enrichment, multiple dispersal events can be captured with this technique through the application of different marks with each recapture. Thus, while more labor intensive due to multiple mark-recapture sampling schedules, a fairly detailed picture of inter-patch dispersal can be obtained. Users of this method must, however, consider several different species-specific factors which

may confound with inferred dispersal events. For example if mortality rate is high relative to the time between recaptures changes in abundance within different patches may be due to death (Turchin and Thoeny, 1993); changes in abundance between sampling also potentially due to differential capture success rates, dispersal only able to be implicated upon the individuals explicit recapture within another patch.

Increasing the degree of specificity in individual tracking, genetic markers such as microsatellite DNA (Semlitsch, 2008) have been used to estimate dispersal/gene flow for over half a century through examining the spatial distribution of genetic variation (Berry *et al.*, 2004). Landscape genetic techniques, for example, use such microsatellite data to determine the genetic differentiation between populations across the landscape calculating FST values, which estimate such differentiation relative to the landscape (Walker *et al.*, 2007), smaller values from pair-wise population comparisons indicating less differentiation and thereby higher rates of gene flow/dispersal (Arens *et al.*, 2007; see Balkenhol *et al.*, 2009 for future directions for landscape genetics). However, as this spatial distribution has been structured through time, recent dispersal cannot be differentiated from historical events. Thereby genetic techniques may be modified through the use of individual based assignment tests which can measure recent dispersal through determining, based on the multi-locus genotype of an individual, the probability that the individual is from a particular population (Berry *et al.*, 2004; see paper for outline of assignment calculations). It must be noted that assignments will have greater accuracy when the genetic variation between populations is large, and therefore this technique may not be appropriate in metapopulations with known high dispersal rates.

While all of the above methods allow some elucidation of dispersal within the system, the information gathered regards only the beginning and end locations of dispersal and not the specific path taken between these points. Thereby the use of

radio telemetry or radio tracking offers a significant advantage in that the entire dispersal event is monitored, individuals being tracked throughout; being considered a measure of actual (realized) connectivity (Calabrese and Fagan, 2004). Indeed implementation of this technique allows researchers to ask detailed questions regarding the direction, distance, and effects of life history characteristics on individual dispersal. Two limitations still exist. Firstly, while the list is rapidly growing due to advancing technology, this method is not suitable/ applicable for every species (e.g., aquatic invertebrates). Secondly, tracking is extremely labor intensive, limiting the number of individuals that can be followed and the duration of tracking; researchers must weigh the tradeoffs between the amount and quality of collected data considering the level of detail that the questions of interest require.

4.5.2 Indirect methods

These methods are largely statistical and concern connectivity metrics; in metapopulation research focusing on patch level connectivity where the colonization of unoccupied patches forms the basis of metapopulation dynamics (Moilanen and Hanski, 2001). Indeed, indirect methods are related to the issues of measuring potential dispersal or connectivity across patches within landscapes since connectivity is a measure of the degree to which suitable habitat patches are also dispersal-suitable and can only be used to infer potential but not realized dispersal. Connectivity, therefore, is essentially a type of inverse function of isolation, with increasing patch isolation related to decreased connectivity (Tischendorf and Fahrig, 2001) and as such, the degree of isolation is often also used within metrics to represent potential dispersal.

At least two different categories of indirect connectivity metrics exist, both based on system spatial structure but differ in the amount of species specific dispersal data incorporated, thereby creating a hierarchy of realism. The first category (most abstracted), structural connectivity measures, incorporates no species specific data, such as dispersal ability, and relies solely on the spatial attributes of the system to confer dispersal probability (Figure 4.1a). The most commonly used distance metric, nearest neighbor, considers the distance between a focal patch and its nearest occupied neighbor ignoring the contribution of all other patches within the system (Calabrese and Fagan, 2004) and assuming that smaller inter-patch distances equate with increased (potential) dispersal. Variants of the nearest neighbor metric also exist which relax "nearest" and incorporate distances to all patches, termed neighborhood matrices. Here a negative exponential function is often used in order to discount potential dispersal from patches at increased distances from the focal patch. Heinz *et al.* (2005) have recently developed an alternative function, which they found to better account for patch accessibility, which factors in the landscape configuration of other patches within the system while discounting between any one patch and the focal patch, as other patches within the system can be viewed as competing with the focal for dispersers, thus affecting its accessibility (see paper for details).

The second category, potential connectivity, includes both structural information and the dispersal ability of the focal species as if the distance between patches is further than the dispersal ability patches are considered unconnected (Calabrese and Fagan, 2004), providing an idea of functional connectivity (see below). However, quantifying dispersal ability is just as difficult as quantifying dispersal and researchers are often limited to using either a fixed distance beyond which dispersal probability decreases, or a randomly chosen value from dispersal kernels (Calabrese and Fagan, 2004; Fagan and Calabrese, 2006; see Skarpaas *et al.*, 2005 for outline of kernel estimation). Several examples of potential connectivity metrics exist. The

graph theoretic metric calculates all possible pair-wise connections between patches using dispersal and GIS (area, shape and spatial arrangement of patches) data (Calabrese and Fagan, 2004; Figure 4.1b). In contrast, the incidence function metric (see below for more details) uses patch occupancy data, considering based on area and distance the contribution of all occupied patches to the connectivity of the focal patch (Calabrese and Fagan, 2004; Figure 4.1c). Similarly buffer radius metrics consider only those patches which supply dispersers using the area of occupied patches occurring within a specified distance (buffer) of the focal patch (Bender *et al.*, 2003; Calabrese and Fagan, 2004; Fagan and Calabrese, 2006; Figure 4.1d).

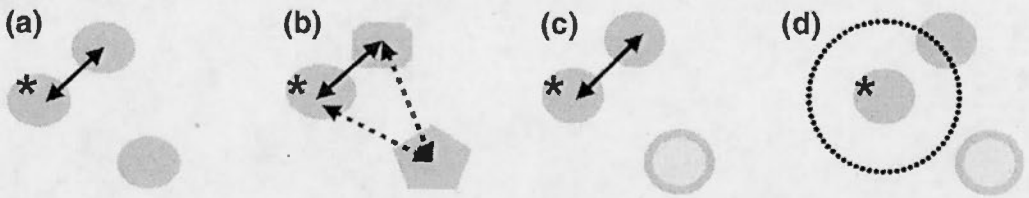

Figure 4.1. Forms of indirect connectivity metrics. Various forms of connectivity metrics used for the indirect quantification of dispersal in metapopulations; two different categories are represented, structural a) and potential b)-d). a) Nearest neighbor metric. Star denotes focal patch, arrow represents dispersal between all patches under consideration, only the nearest patch. b) Graph theoretic metric. Patches differ as data is obtained from GIS, potential connections between all combinations of patches are considered, dashed arrows represent connections not established because outside of focal species dispersal range. c) Incidence function metric. All combinations of patches which are occupied are considered, here light coloured patch denotes empty. d) Buffer radius metric. The area of all occupied patches which fall within the dispersal range of the focal species are considered, dispersal range represented by dashed circle. Adapted from Calabrese and Fagan (2004).

As much metapopulation research has measured dispersal using incidence functions (IF) this measure warrants further discussion, especially in the case of metacommunities. As mentioned above, dispersal (colonization) within IF is modeled

by patch isolation (Hanski, 1998), within a function considering the number of immigrants into the patch and a constant. In order to derive parameters for these models, snap shot data from mark-recapture studies is used thereby only capturing information of the system at one point in time (see Hanski, 1994a; Hanski *et al.*, 1996 for parameter estimates). While this may cause problems (discussed below), IFs may be iterated to predict system dynamics and patch occupancy patterns at final equilibrium (Hanski, 1994b; Hanski *et al.*, 1996). An additional potential problem with IFs is the failure of the likelihood maximization algorithm to converge, which becomes amplified in the case of multi-species systems and therefore may exclude IFs from being adaptable to metacommunities.

Lastly, and following for any indirect method, complications may arise depending on how well species are distributed within the landscape. For instance, although common species most likely disperse, a spatial signal may not be captured as the species will be present throughout the system, patches appearing as if highly connected even though individuals may not have large dispersal ranges; rare species, on the other hand, limited to a small number of sites, may present an important spatial signal (e.g., if limited to a small area) but will have low rates of dispersal between patches.

Such measures which factor in species specific information allow for the understanding of the functional connectivity of the landscape, integrating landscape characteristics as well as species preferences and behavior (Pinto and Keitt, 2009). Indeed not only may dispersal abilities or threshold distances be incorporated, but also the permeability of the landscape matrix through which the organism must pass, considered part of the species behavior (see Baguette and Van Dyck, 2007). The degree to which landscape characteristics are permeable according to the species depends both upon the size of the functional grain, the smallest spatial scale at which

the organism can perceive spatial heterogeneity according to its range (Baguette and Van Dyck, 2007) and also the suitability of such perceived characteristics.

While it is Euclidean distances which are often used within connectivity metrics, matrix heterogeneity and permeability (resistance) is incorporated through the use of least-cost analysis which assigns cost values to each cell between the source and target based on landscape characteristics and associated species preferences (e.g., importance of landscape geology for connectivity of rock-dwelling mountain vizcacha (*Lagidium viscacia*) in Walker *et al.*, (2007)). Here the effective distance of the path needed to reach the target with the least cost, or the cumulative cost of a particular path is used to assess the connectivity (Broquet *et al.*, 2006), increased values equating with decreased probability (Bender and Fahrig, 2005; Driezen *et al.*, 2007; see references and O'Brien *et al.*, 2006 for detailed outline). Such least cost paths often cluster forming dispersal corridors, with the particular path used within the corridor potentially differing based on dispersal behavior, corridor breadth thereby potentially affecting connectivity (see Pinto and Keitt, 2009 for corridor determination). Despite their utility it must be noted that least cost analyses require data regarding dispersal ability through different landscape components, which may be unknown and difficult to determine (Broquet *et al.*, 2006), and assume that the disperser has complete knowledge of the landscape and uses this information to choose dispersal routes (Baguette and Van Dyck, 2007), which may not be valid due to limited perceptual range.

4.6 From metapopulation to metacommunity dispersal

Clearly the presence of multiple species within metacommunities, unlike metapopulations, complicates or perhaps even impedes the application of direct

dispersal measures as we may not be able to capture dispersal for multiple species simultaneously. Indeed, for direct quantification techniques to be developed, or those used for metapopulations adapted, the sampling intensity needed to capture all species within the system will have to be seriously called into question; common species will be found throughout the system, however rare species will be harder to capture while having a large affect on local system structure. Thereby, within metacommunity research we may have no other option (at least currently) than to resort uniquely to indirect methods which are often highly simplified from ecological reality (see Schumaker, 1996 for a discussion). What must start to be questioned with the increasing use of the metacommunity paradigm is whether these methods are sufficient for quantifying dispersal, if direct methods can be derived from those currently used within metapopulations and, should we be left without the possibility of direct methods, can indirect methods tackle the mutually exclusive competing hypotheses that can be evoked to explain metacommunity structure (see below).

It would be possible, although feasibility will be left up to the independent researcher and the specifics of the system, to adapt several of the direct methods currently available within metapopulations for implementation in metacommunity situations. Isotope enrichment certainly could be performed in a metacommunity of aquatic invertebrates; keeping in mind that sampling range would have to be adapted to account for variance in dispersal range between species. Radio telemetry could be utilized, however, due to the tracking of multiple species researchers would have to adapt relocation parameters as some species may move greater distances, at different times of the day, or at different rates. Likewise, other mark recapture techniques could be applied within metacommunities such as the tagging and recapture of individuals, however, with the same considerations. Genetic markers could also be used for multiple species provided that genetic information is available; for many species markers have not yet been developed thereby incurring increased cost and

time (Berry *et al.*, 2004).

Currently, two classes of indirect methods have been put forward to study metacommunities, the first is based solely on the geographical arrangement of sites whereas the second uses information on the degree of patchiness of the metacommunity. The first class uses spatial predictors to cast on autocorrelation patterns in the distribution of metacommunities. The predictors range from simple geographical coordinates, latitude/longitude, to more sophisticated such as geographical polynomials and orthonormal transformations such as eigenvector maps and splines (Griffith and Peres-Neto, 2006). For example, Vanschoenwinkel *et al.* (2007) in their study of aquatic invertebrates inhabiting a system of 36 rock pools calculated a distance matrix which contained the distances between each pair-wise combination of patches and in the 158 data set meta-analysis of Cottenie (2005) distance between patches within each data set was inferred through use of spatial polynomials.

The second class regards methods for the quantification of dispersal which allow the incorporation of species data for metacommunities within indirect metrics and hence are extensions of those used for metapopulations. Fagan and Calabrese (2006) outline two such methods. The first uses species-specific data from an umbrella species and may be applied if all species within the system have similar dispersal abilities and habitat preferences. The umbrella species is that which is chosen to represent all species within the system, and therefore should have the smallest dispersal ability so that all other species within the community have higher levels of dispersal, leaving the value of connectivity (potential dispersal) conservative (Fagan and Calabrese, 2006). If habitat preferences are the same but dispersal abilities differ then Fagan and Calabrese (2006) propose the use of a second method, range bounding, where dispersal abilities of species within the community are determined and dispersal

across the community is considered through means or dispersal thresholds. While these two methods are certainly an improvement over the first class of indirect methods due to the incorporation of species data, they are still limited in their consideration of only representative species specific data rather than the actual consideration of all species within the community. It must be questioned, therefore, whether such methods are able to properly account for the role of dispersal in determining community composition (see below).

4.7 Current challenges and considerations

While dispersal acts to spatially structure communities (Bahn *et al.*, 2008), their spatial structure does not depend uniquely upon dispersal between sites but also on factors such as the spatial structure of the environment, biotic interactions, the magnitude of temporal stochasticity in environmental variation (Heino, 1998), among others. The fact that some ecological factors other than dispersal may also lead to spatial signatures complicates the goal of many metacommunity studies, i.e., to understand the relative importance of different structuring factors such as dispersal and environment (Cottenie, 2005; Legendre *et al.*, 2002; Leibold *et al.*, 2004), especially when indirect methods are applied. In fact, just as it is intuitive and assumed (within connectivity measures) that those patches which are closer together should have higher levels of dispersal, it is also intuitive that they should share similar environmental characteristics (temperature; i.e., positive spatial autocorrelation). Thereby, space itself acts to structure the system as do both environment and dispersal which themselves are spatially structured. For example, the occurrence of the same species on two close patches could be due to the ease of dispersal between them due to spatial structure, and/or due to the common favorable environment which may be spatially structured (Dieckmann *et al.*, 1999; Wagner and Fortin, 2005). A potential problem therefore arises; since indirect methods for

measuring metacommunity dispersal, the only current option, are largely if not solely dependant on the underlying system spatial structure, it is possible that the measure of dispersal may also represent other likely, but unmeasured, underlying factors that also happen to be equally spatially structured. For example species may be distributed among patches not due to dispersal but the local environment, arriving at patches in which they are ultimately not found due to unsuitable local conditions, with, then, spatial distribution not capturing actual dispersal events but rather spatially structured environment. Therefore, by using indirect methods, we may have problems in determining the likelihood of competing hypotheses (e.g., dispersal versus environment) to explain particular patterns in metacommunity structure; seriously calling into question the utility of current methods, and the degree to which measured dispersal is dispersal at all.

One technique which has been used within many studies to disentangle the effects of space and the environment has been variation partitioning applied to canonical analysis (e.g., redundancy analysis, canonical correspondence analysis). This technique decomposes the total variation in community distribution (composition or abundance) into variation explained by components of space [S] and environment [E] (Borcard *et al.*, 1992; Peres-Neto *et al.*, 2006); that explained by pure environmental variables [E|S], purè spatial variables [S|E], a common component, spatially structured environment [EwS] and the remainder, unexplained or residual variation (Figure 4.2a). Within variation partitioning information on the geographical distribution of sites is used to represent [S]. Despite this, variation partitioning has been implemented quite often within metacommunity research (Cottenie, 2005; Gilbert and Lechowicz, 2004; Tuomisto *et al.*, 2003) to help distinguish between four metacommunity models: neutral with homogeneous E and strong S structure of functionally equivalent species, patch dynamic incorporating a colonization/competition tradeoff, species sorting with heterogeneous E and slight S

structure and mass effect increasing the importance of S (Cottenie, 2005; Ellis *et al.*, 2006). Here many researchers are tempted to equate [S] with dispersal. While it is easy to understand why this is done, as dispersal is so intertwined with space (i.e., [S]), equating these two in relation to variation partitioning both misrepresents how it was formulated and the information it provides. For instance, if variation partitioning indicates that [E|S] is not significant but [S|E] is, one may be inclined to deduct that the structuring mechanism is neutral dynamics. However, [E|S] does not consider all possible important environmental factors and [S|E] could easily include unmeasured spatially structured environmental variables which are important for metacommunity structure. Variation partitioning, therefore, should be extended to include dispersal. This extension would allow researchers to decompose community composition variance into all three structuring factors thereby potentially explaining more of the often large residual variation (Figure 4.2b) and force dispersal quantification to go beyond the attributes of the system, so that space and dispersal are measured differently.

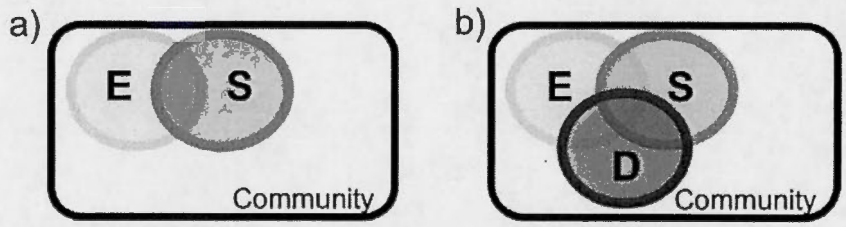

Figure 4.2. Variation partitioning. Theoretically the amount of variation in community composition, represented by the area within the box, explained by: a) components within the original variation partitioning technique, where E represents environmental variables and S spatial variables; b) the components of the extended variation partitioning technique where D, dispersal, is added thereby explaining additional community variance not accounted for by a). Size and degree of overlap among circles in both a) and b) do not reflect the amount of variation that is explained as realistically not all components will be equal. Adapted from Borcard *et al.* (1992).

Temporal heterogeneity is also an important structuring factor within metacommunities. As the majority of ecological research is conducted over short time periods, largely not longer than 1 or 2 years, it is also not often considered properly or fully within ecological studies, and quantification methods may not properly, then, account for temporal heterogeneous dispersal, or other heterogeneity. There is, obviously, a strong need to do so as if the metacommunity is sampled at two time periods differences in abundances or community composition may not be due solely to dispersal to or from patches but also mortality, reproduction or even the emergence of individuals already in the community (e.g., from seed banks). Such phenomena would not be accounted for through indirect methods (since individuals are not directly tracked) and such changes would be attributed to dispersal. In fact within metacommunities, the relative influence of all three structuring factors, environment, spatial other than dispersal and dispersal, may change through time. In addition to changing in strength, the influence of these structuring factors may rotate through the system. Consider a metacommunity which changes from species sorting to patch dynamics from year 1 to year 2. If only a subset of the patches is considered, it may appear that E is no longer important. However, following from the concept of edge effects (Figure 4.3a) E may still influence those patches indirectly through influencing the species that could potentially immigrate if it has switched to other patches still within the system (Figure 4.3b). Therefore, in order to fully understand the effects of dispersal, the effects of temporal heterogeneity upon system dynamics and dispersal itself should also be considered, and quantification methods developed which can handle this added complexity.

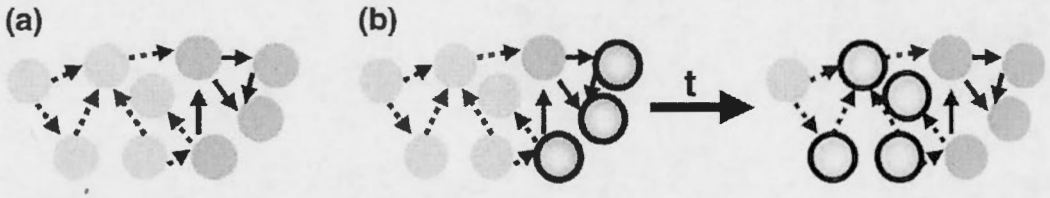

Figure 4.3. Partial systems and shifting influences. Three different forms of a system, complete system is all interconnected patches (CS), partial system (PS) are dark colored patches and the light colored patches are the rest of the system (RS). PS is that under consideration within a study and therefore only solid arrows are considered, dashed arrows are dynamics which occur outside of consideration. a) edge effects, patches within PS are still affected by immigration and emigration from the RS. b) temporal heterogeneity where over time the part of the system which is influenced by a variable, patches with white centers, shifts. Although outside of the area of consideration the variable still affects both the CS and indirectly the PS through dispersal.

4.8 A wishlist and future technical advancements

Will ecologists ever be able to overcome the logistic and methodological challenges involved in estimating dispersal in metacommunities? Certainly there are still several major hurdles to overcome. Firstly, although within both metapopulations and metacommunities it is the application of indirect methods which are most prevalent, further attempts at modifying metapopulation indirect methods, such as robust connectivity metrics in which species-specific data is incorporated, to be applicable in metacommunity situations beyond the use of only representative species information should be made. This would afford researchers working within metacommunity systems more options for quantifying dispersal when the use of indirect methods is sufficient to answer the questions of interest.

Likewise, although several different direct methods for quantifying dispersal are available within metapopulation research, each with its own set of limitations, no direct methods currently exist for metacommunities. As it could be argued that accurately representing dispersal within metacommunities is even more important than in metapopulations due to issues of species interactions and coexistence, it is extremely necessary that methods for the direct quantification of dispersal within metacommunities be developed. As previously discussed, it is conceivable, although feasibility would have to be evaluated, to adapt metapopulation direct methods for implementation within metacommunities.

In addition, although dispersal and other spatially organized factors are often equated they are, in fact, separate factors which both act in spatially structuring the system. Therefore extension of the variation partitioning technique to include dispersal is necessary in order for the variance in community composition to be decomposed into all three structuring factors to which it can be attributed. Lastly, as temporal heterogeneity may cause these factors to change in importance or shift in influence through time its effects must be taken into consideration in order to properly account for system dynamics. Indeed the indirect methods currently available, which are largely dependant on the spatial structure of the system, will not accurately capture dispersal when the system varies temporally, as all changes will be attributed to dispersal; such a problem would be circumvented if direct methods, such as radio-telemetry were employed. Thereby, there may be cases where it is necessary, despite the technical difficulties, for direct methods to be employed within metacommunity research; such methods however, must first be developed.

Therefore, although we have come a long way in our understanding of metapopulation and metacommunity systems and the underlying factors which act to structure them, there clearly is still a long way to go before the insight we gain

through empirical studies is able to be directly relatable to the dynamics of natural systems. We certainly believe that some questions regarding the importance of dispersal in structuring metacommunities can be answered, some may and some may not be able to be answered with current dispersal quantification methods. We invite ecologists to classify their questions into these three categories as this may help in understanding the limitations and generality of the conclusions reached and elucidate ways to best overcome the current technical challenges to develop methods that can best answer questions of interest.

CONCLUSIONS

As previously mentioned, the overall goal of this thesis was to determine the functionality of intra-specific variation and investigate the degree to which an individual's phenotype influences its distribution within and across different environmental conditions. Such phenotype-habitat relationships were explored across three experimental chapters which all investigated the potential for morphology, as well as both biotic and abiotic factors, to influence movement and structure distribution across stream habitats; chapters differing in the primary conceptual underpinnings and scale at which such patterns were considered. The final chapter of this thesis was, in contrast, a perspective paper outlining the current methods for (or lack thereof) and challenges faced in quantifying dispersal through systems at larger metacommunity spatial scales, discussing the difficulty in differentiating distribution patterns due to dispersal versus system spatial structure and environmental characteristics.

Within chapter I, the potential for the generation of fitness variation within a population was explored, experiments interested in the distribution of individuals across resource patches within an artificial stream channel. Here it was found that the spatial distribution of resource patches, a previously overlooked structuring factor, and population density interacted to produce different degrees of growth variation as a function of changes in the type of competition utilized (i.e., agonistic versus scramble); within-trial growth variance decreasing at low but increasing at high population densities as patches became more clumped. Despite feeding trials being conducted within a laboratory setting, using stationary rather than drift feeding, this result has potential implications for stream restoration decisions. Indeed, since different degrees of variance were found at the same density level as a function of spatial resource distribution, restoration efforts should strive not only to ensure an

adequate resource supply to support density goals, but that those resources are distributed to some degree across the system, dispersed feeding trials within this chapter associated with less growth variance and therefore less pressure for population regulation (i.e., emigration, mortality) within the site. As here both pre- and post-trial morphology were found to be related to an individuals ability to compete (i.e., grow), and competitive morphologies were those reflecting greater swimming capacity and efficiency, individuals re-distributing themselves within natural systems during such often reported density-dependent population regulation may represent a specific subset of the phenotypic diversity within the system.

The potential for and process of phenotype sorting and non-random movement to structure distribution as a function of habitat type (i.e., environmental characteristics) and density was further and more directly explored within chapters II and III, at the scale of individual movement across habitat sections within an artificial stream and community level re-assembly (re-colonization) across a defaunated natural stream reach, respectively. Within both chapters, individuals selecting different habitat sections/types were found to be morphologically differentiated indicating a degree of environmental filtering, the morphological adaptations of individuals (or species) found within each habitat type reflecting their increased ability and capacity to use such sections (adaptive habitat matching). In the case of chapter II, while the degree of phenotypic differentiation between habitat sections decreased as density increased, differentiation remained significant and individuals continued to non-randomly sort/move while making habitat selection decisions based on their relative competitive abilities within original habitats; the frequency-dependent game model developed upholding that phenotypes had different habitat preferences with only one being dispersal-biased as a function of density. With respect to chapter III, the novel goal of which was to bridge the gap between trait-based community structure and composition-based temporal trajectory categories of assembly literature,

morphologies found within different habitat types were significantly differentiated, returning deterministically towards pre-disturbance morphological composition through time, such patterns found at both the overall stream community as well as component species levels.

Additionally within both chapters II and III, the degree of such phenotype-dependent habitat selection and differentiation was found to be species-specific, dependent on the swimming propensity/capacity (i.e., mid water-column versus benthic) of the species utilized. Within chapter II blacknose dace, a mid water-column riffle species, was found to be, and remain, the most morphologically differentiated between habitat sections across density levels compared to both benthic species, mottled sculpin (riffle) and johnny darter (pool). Within chapter III creek chub, a mid water-column pool species, was found to be comparatively more differentiated both between habitat types and through re-assembly than longnose dace, a benthic riffle species. Taken together these results indicate a greater sorting and filtering of mid water-column individuals across habitat types due to the selectivity and energetic demands faced as a function of water velocity; benthic species on the other hand less differentiated across habitats, morphologies more interchangeable, due to the lesser energetic constraints of buffered velocity. It must also be noted that all of the above phenotype-habitat distribution patterns, for chapters I, II and III, were found to be a function of only morphology, this factor and not fish size/length, as is currently proposed, dictating relative competitive ability and movement through/use of habitat types; the intra-specific variation found, while only detectable with the use of multi-variate statistics, still ecologically significant, influencing individual fitness and distribution. Such results indicate that habitat managers should, as well as considering the spatial distribution of resource inputs, be aware of the potential influence of the properties (i.e., water velocity) and spatial arrangement (i.e., pool, run, riffle ordering) of habitat types for the ability of different species to move across and re-colonize potentially

newly formed or restored habitats. Indeed as morphologies of even the same species were found to be significantly differentiated across habitats, the mere availability of a new site may not lead to its use if the phenotypes available within the system are not compatible.

In conclusion, the potential importance and structuring influence of intra-specific variation has only recently, largely during the time-frame of this thesis, started to be recognized and gain attention, not as of yet fully incorporated within community ecology. Thus there still exists much work to be done, at both the community as well as population levels, the potential next steps resulting from the experimental chapters presented here being: 1) to investigate the combined influence of spatial resource distribution and patch quality variation, at laboratory as well as natural stream scales (chapter I), 2) to explore phenotype-dependent habitat selection in a multi-species context in addition to the fidelity of and explicit fitness consequences resulting from habitat use decisions at both multi- and single-species levels (chapter II), 3) to understand how component species (i.e., population structure) add to determine overall community trait relationships and the variable influence of biotic and abiotic factors at both community and population levels (chapter III); and, with respect to chapter IV, 4) to attempt to modify (from metapopulation) and produce direct and indirect methods for measuring dispersal at metacommunity scales so that dispersal, as well as temporal heterogeneity, can be more accurately accounted for as structuring factors. It is the hope that the research in this thesis will inspire and advance the use of a trait-based ecology that explicitly incorporates intra-specific variation, allowing for a more accurate and complete understanding of the patterns in and processes underlying species and individual distribution across heterogeneous landscapes.

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